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The Effect of Food on Reproduction in the Sailfin Molly, Poecilia Latipinna (Poecilidae)

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THE EFFECT OF FOOD ON REPRODUCTION IN THE SAILFIN MOLLY, *POECILIA LATIPINNA* (POECILIIDAE)

BY

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THESIS

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ABSTRACT

Sailfin molly populations often experience a midsummer slump in reproduction, and it has been suggested that this slump is caused by food shortage. A food supplementation experiment on a natural population of mollies was done in 1983. Excess food did not directly affect the fecundity of females in the field. A laboratory experiment was designed to determine the effect of food level on reproduction in females. Ration had the greatest effect on somatic condition and growth, indirectly influencing fecundity. Two explanations for this strategy are suggested. A significant difference in brood size and size of young was observed between the field and lab broods at all ration levels. The possibility of plasticity being an integral component of the sailfin molly's life history strategy is discussed.

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This work is dedicated with love to my husband, Richard E. Smith.

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INTRODUCTION

The life history strategy of any organism revolves around its need to maximize lifetime reproductive fitness (Pianka, 1976). The maintenance and growth of the soma are vital to overall fitness, but only to the extent that they affect future reproduction (Williams, 1966; Gadgill and Bossert, 1970). Since most organisms live within the bounds of finite resources, reproductive interests must compete for those resources with somatic processes. Energy spent on current reproduction is energy that cannot be used for maintenance or growth, resulting in decreased future reproductive value (Fisher, 1930; Calow, 1979). The manner in which energy is partitioned to produce the greatest number of viable offspring over the lifetime of the individual is a major determinant in defining its life history strategy.

The calories used for the production of young must come from one of three sources: 1) directly from ingested food; 2) from energy that has been stored as lipids; or 3) from energy that has first been converted to soma as structural proteins (Pianka, 1976). Numerous studies have shown that reproductive output is influenced by the quantity of food ingested (e.g., Ivlev, 1961; Bagenal, 1969; Schoener, 1971; Giesel, 1976), and there is also evidence that the quality of food may be equally critical (Bradley and Mauer, 1971; White, 1978). In the first book written on animal ecology, Elton (1927) recognized feeding as "the primary driving force of all animals" and believed that food supplies regulated the structure and activities of entire communities. The gathering, manipulating,

and ingesting of food may occupy the majority of an individual's lifetime, and efficient use of this energy has been a focal point for natural selection.

The literature dealing with the effects of food on reproduction points out the variety of mechanisms that exist for coping with or exploiting variable ration levels. Among invertebrates, insufficient food results in fewer young and longer intervals between reproductive episodes for a predaceous mite (Rivard, 1962), in barnacles (Calow and Woollhead, 1977), and brine shrimp (Browne, 1982). High rations result in more young (Rivard, 1962; Browne, 1982), and Crisp and Patel (1961) found that a greater percent of a barnacle population became reproductive under favorable resource conditions. Variable food levels also affect the somatic parameters of many invertebrates. Low rations slow growth rates in barnacles (Barnes, 1962; Calow and Woollhead, 1977), while high rations increase growth rates, improve somatic condition, and increase lifespan (Coe, 1947, in the Pismo clam; Crisp and Patel, 1961; Barnes, 1962; Rivard, 1962; Calow and Woollhead, 1977; Browne, 1982).

Vertebrates also show a variety of responses to fluctations in ration. Elk (Thorne et al., 1976) and tree lizards (Ballinger, 1977) exposed to low resource conditions reproduce less often, have smaller young or eggs, and/or their overall reproductive effort is below average. Nagy (1973) found that growth of a desert lizard is stunted in low food situations. High food levels produce faster growth, greater storage of body fats, improved somatic condition and the production of more young per season in Merriam's kangaroo rat (Bradley and Mauer, 1971) and tree lizards (Ballinger, 1977).

The literature on food and reproduction in fishes is massive, and few generalizations can be made. It appears that in many species, ingested food has an immediate effect on fecundity, either directly through the number of eggs or young produced (e.g., Scott, 1962; McFadden et al., 1965; Bagenal, 1966, 1967; Lyagina, 1975; Tyler and Dunn, 1976; Townshend and Wootton, 1984), or indirectly through adjustments in other reproductive parameters, such as the number of maturing oocytes produced (Robb, 1982; Townshend and Wootton, 1984) or the size, weight, or condition of eggs or young (Nikolskii, 1962; McFadden et al., 1965; Wootton, 1973, 1977; Hislop et al., 1978; Constanz, 1979). Ration level may also effect the gonads of adults, with high food levels increasing ovary weight (Nikolskii, 1962; Tyler and Dunn, 1976; Hirshfield, 1980; Townshend and Wootton, 1984) or low food levels initiating gonadal regression (deVlaming, 1971). Scott (1962) and Robb (1982) demonstrated increased resorption of developing ova as a result of limited food. The age and size of females at maturity may vary related to ration (Nikolskii, 1962; McFadden et al., 1965; Wootton, 1973), as may population responses in the percent of females that become mature (Scott, 1962; McFadden et al., 1965; Bagenal, 1969). Wootton (1973, 1977, 1979) and his collegues (Wootton et al., 1980; Townshend and Wootton, 1984) have shown in numerous studies that three-spined sticklebacks can adjust their interspawning interval in response to food levels. This allows them to significantly increase the number of spawnings per season under favorable resource conditions and prolong their breeding season past the average time restrictions.

Many fish increase their future reproductive potential by investing excess resources into their soma. High food levels have been shown to increase growth rates (Tyler and Dunn, 1976; Constanz, 1979; Hirshfield, 1980; Townshend and Wootton, 1984) and improve overall physical condition (Bagenal, 1969; Hislop et al., 1978; Constanz, pers. comm.). Low rations decrease growth rates (Nikolskii, 1962; Tyler and Dunn, 1976; Hirshfield, 1980; Wootton et al., 1980), somatic condition (Hirshfield, 1980), and energy stores (Constanz, pers. comm.).

Fishes of the family Poeciliidae produce live young and exhibit varying degrees of viviparity (Thibault and Schultz, 1978), characteristics that make them ideal for examining aspects of reproductive energetics. However, surprisingly little work has been done in this area. Meffe and Vrijenhoek (1981) examined the effects of starvation on three species, Poeciliopsis monacha, P. prolifica, and Poecilia reticulata. These species maintain their reproductive output regardless of ration level, sacrificing body mass if necessary. In the guppy (Poecilia reticulata), limiting the food supply directly and immediately decreases fecundity (Hester, 1964). Reduced rations also affect the size of future broods by decreasing the number of maturing oocytes but has no effect on the size of young or the interbrood interval (Hester, 1964). Reznick (1983) found that guppies store most excess energy as fats, which may be used to improve fecundity or survivorship. In the mosquitofish, Gambusia affinis, food level has a direct effect on reproduction, producing quick adjustments in the number and weight of young (Dionne, 1985; Meffe, 1986).

Poecilia latipinna, the sailfin molly, is an ovoviviparous (lecithotrophic) livebearer; its embryos develop primarily from energy contained in the egg yolk, with little or no maternal contribution of nutrients after fertilization (Turner, 1940). Although some poeciliids display superfetation, the sailfin molly does not fertilize a clutch of eggs until several days after the birth of the previous clutch (Hubbs, 1964; Snelson et al., 1986). Brood size may vary from less than five to over 100 young (Snelson, 1980), and interbrood intervals range from 26-50 days, with an average of about 34 (Snelson et al., 1986). Well-developed, free-swimming neonates are produced and there is no parental care after parturition.

The sailfin molly is a small fish, rarely exceeding 8 cm total length. It inhabits fresh and brackish water from South Carolina to the Yucatan Peninsula of Mexico (Rosen and Bailey, 1963), and is common in a variety of shallow, vegetated habitats throughout Florida. The diet consists primarily of detritus and periphytic algae (Harrington and Harrington, 1961). It derives its common name from the expansive, brightly-colored dorsal fin characteristic of large males (Snelson, 1985).

In east-central Florida, the sailfin molly usually has a spring and fall peak in reproduction with a period of depressed reproduction in mid-summer (Snelson, 1980). Hubbs (1964) attributed late summer reproductive senility of Poecilia latipinna to reduced food availability brought about by decreasing photoperiod. Wetherington (1982) studied the energetics of reproduction in this species and suggested that mollies went through a severe resource bottle-neck in late spring and early

summer that influenced subsequent reproductive output. The objective of my study was to evaluate the impact of food resources on molly reproduction as follows: 1) to measure and describe reproduction and growth in female sailfin mollies subjected to three different diet rations in the laboratory; 2) to examine the effects of maternal diet ration on the number, size, and condition of broods at parturition; and 3) to supplement the diet of a natural population of mollies, comparing measurements of size and reproductive status with those of a control population.

MATERIALS AND METHODS

Field Experiment

The field study designed to assess the effects of food supplementation on reproduction was carried out near the Kennedy Space Center in Brevard County, Florida. The study site, nicknamed Badge Station, was a network of brackish water borrow ditches adjacent to the Indian River lagoon (T22S, R35E, Sec.36). Molly populations at this site have been studied by researchers from the University of Central Florida since 1978. Physical parameters for April through September 1983 are given in Appendix Table 1. Water temperature was taken at the surface with an immersible thermometer. Refractive index was measured with an optical refractometer and converted to salinity (ppt). Changes in water level were monitored with a pvc stand pipe permanently placed in one ditch.

In June 1983, separate, but concurrent, experiments were carried out in two ditches at Badge Station. Each experiment consisted of a feeding area and a control area, with a buffer zone separating them (Figure 1). The areas were blocked off from shore to shore with 0.32 cm mesh nets that effectively confined adult mollies. The nets were secured to the shores and to the bottom with ropes and weights. The tops of the nets were held above the water by pvc pipes. A 92 x 94 cm floating feeding box made of wood and covered with small mesh wire was anchored near the center of each feeding area. By using a feeding box, the added food was confined and did not float into the buffer zones or control areas. Directly under each box, a large sheet of plastic was held on the

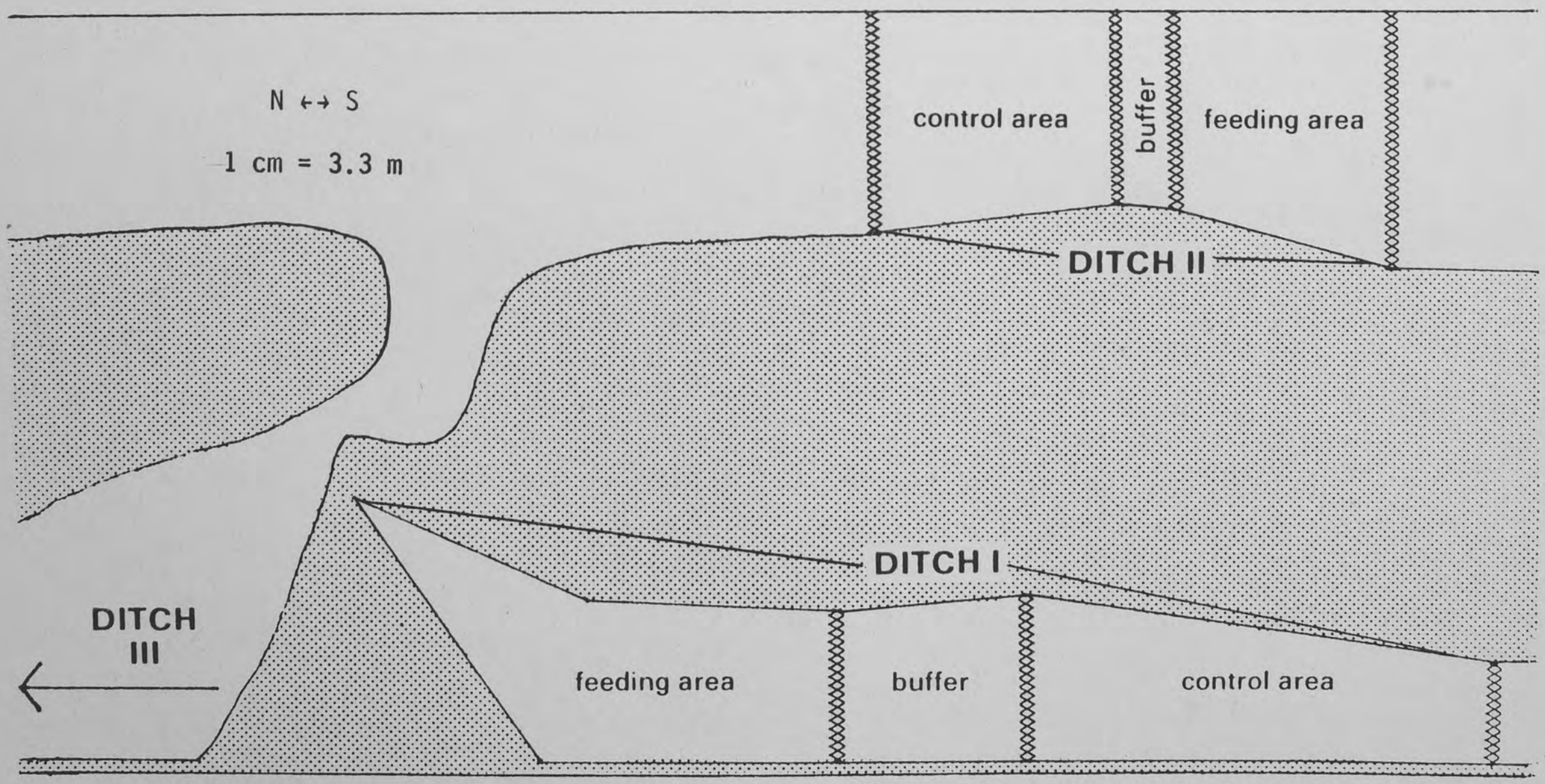

FIGURE 1. Badge Station field experiment site. Stippled areas represent land; clear areas represent water; cross-hatching represents block nets.

bottom by weights so any food that sank before it was eaten would not be lost in the silty substrate.

All fish samples were taken using a seine 3.5 m long x 1.3 m deep, with a 1/2 cm mesh. Large female mollies were anesthetized with MS 222 and measured in the field to insure that the sample included at least 30 females between 37-50 mm total length (TL). All fish collected (males, females, and juveniles) were preserved in 10% formalin. The first sample was taken on 14 June before the ditches were partitioned and before food supplementation began. The block nets and feeding boxes were then put into place.

Feeding began on Wednesday, 15 June, and continued every Monday, Wednesday, Friday, and Sunday for six weeks. Each day, 100 g of Tetramin Staple flake fish food were transferred from shore to the feeding box via a can on the end of a long pole. Tetramin Staple has proved to be an excellent diet for this species in our laboratory. Since I had no estimate of how many fish inhabited the ditches, the 100 g quantity was determined primarily as a guess that was constrained by the cost of the food.

The final feeding was on 31 July. Two days later, 2 August, another sample of at least 30 females between 37-55 mm TL was taken from each control and each feeding area in the same manner as the June sample. The feeding boxes and plastic sheets beneath them were removed, but the block nets were left in place. On 14 September, six weeks after supplemental feeding ended, a final collection was made from each control and feeding area. The block nets, cinderblocks, and pvc pipes were then removed.

In order to assess the background population parameters of the field site, samples were taken from another ditch that was contiguous with the experimental ditches (Ditch III in Figure 1). Monthly collections were made from April through September 1983. An effort was made to sample all microhabitats so that a representative sample was obtained. All mollies caught were preserved.

Females collected during the food supplementation experiment were measured to the nearest 0.1 mm standard length (SL) with dial calipers under a dissecting microscope. Each fish was cut open and the ovaries were characterized as follows: Condition 1, immature; Condition 2, with maturing eggs; or Condition 3, with mature eggs or embryos (after Snelson, 1980). Condition 3 ovaries were removed and teased apart. The propagules were counted and assigned to one of the following developmental categories: Stage 1, mature but unfertilized eggs; Stage 2, early development embryos; Stage 3, mid-development embryos; or Stage 4, late development or term embryos (Snelson, 1980). The number of unfertilized eggs and visually abnormal embryos were counted in Stage 3 and Stage 4 broods.

A somatic condition factor for the reproductive females was calculated from a subsample of 20 from each area in each month. If there were fewer than 20 fish in the sample, all fish were used. SL was measured to the nearest 0.1 mm and the females were dried to a constant weight at 60 C and weighed on a digital microbalance to the nearest 0.01 mg. The condition factor was calculated as (mg dry weight/mm^3) x 10^{-3}.

Mollies from the monthly collections were counted and sexed. Fish that could not be sexed from external characteristics were dissected and

the gonads were examined. A random subsample of 30 females between 18-45 mm SL was selected from each monthly sample. Females within this size range are known to be sexually mature (Snelson, 1980; Wetherington, 1982). These females were measured to the nearest 0.1 mm SL and autopsied. Their ovaries were assigned to a condition category and their broods were counted and staged as above. Some monthly samples did not contain 30 females 18-45 mm SL. In those cases, all females in the size range were used.

Laboratory Experiment

On 25 August 1984, 90 pregnant female and 35 mature male mollies were collected from a site nicknamed VABI (T22S, R37E, Sec.12), a brackish water impoundment near the Badge Station site. A complete description of this site is given by Large (1985). The fish were returned alive to the Ichthyology Laboratory at UCF, placed in several 38 l holding tanks (salinity 6-8 ppt, temperature 27±0.5 C), and allowed to acclimate. They were fed ad lib with Tetramin Staple flake fish food. After two days, the females were anesthetized with MS 222, weighed to the nearest 0.01 mg on a digital microbalance, and measured to the nearest 0.1 mm SL under a dissecting microscope.

Thirty-nine fish 28-35 mm SL were selected for the experiment and randomly assigned to one of three feeding treatments. Each fish was isolated in a 19 l tank equipped with a submersed heater and external motorized filter. Salinity was adjusted to 6-8 ppt with commercial sea salt mix, temperature was held at 27±0.5 C, and photoperiod was 14L/10D. Each fish was fed once daily ad lib until it delivered the brood it was carrying when it was collected (the field brood). Tanks were monitored

in the morning and in the evening for the presence of young. Broods were preserved in 10% formalin immediately upon discovery.

Twenty-four hours after the birth of the field brood, females were anesthetized, weighed, measured, and returned to their home tank. Two mature males were added to each female's tank for 48 hours to insure fertilization of the next clutch. Each female's ration was calculated on the basis of her post field-brood weight. Low ration fish were fed 12% of their body weight per week, average ration fish received 25% of their body weight per week, and high ration fish received 50% of their body weight per week. The food, Tetramin Staple, was weighed once a week and fed in approximately equal alliquots daily.

This feeding regimen continued until the first laboratory brood (lab brood 1) was born and preserved. The day following parturition of lab brood 1, the female was anesthetized, weighed, measured, and mated. A new ration was calculated based on her post lab-brood 1 weight. The ration level (low, average, or high) remained unchanged. The new food ration was delivered each morning until the second laboratory brood (lab brood 2) was born and preserved, after which the female was anesthetized, weighed, measured, and preserved.

Somatic condition factor for females was calculated as (g wet weight/mm^3SL) x 10^{-5}. Relative growth rate for length was determined by log(post lab-brood SL)-log(post field-brood SL)/interbrood interval. Relative growth in weight was calculated in the same manner, except that wet weight was substituted for SL in the formula above.

Each brood was counted and the propagules classified as normal young, abnormal young, or unfertilized eggs. Neonates that were actively

swimming and typically developed were tallied as normal. Normal young in each brood were weighed individually (wet weight) on a digital microbalance to the nearest 0.01 mg. Young that had been damaged by the female or during handling prior to preservation were not included. Brood weights were calculated by multiplying the average weight of young in the brood by total normal young.

Due to the large number of immature and/or abnormal young born in the second lab broods, the data from this portion of the experiment were excluded from analysis (Appendix Table 2). Anomalous young were produced at all diet regimes and, therefore, the effect did not appear to be related to ration level. The cause of these abnormal young was not determined and we have not seen this phenomenon previously in other laboratory experiments with this species (Wetherington, 1982; Large, 1985; Snelson et al., 1986).

Condition factors for the field experiment fish were calculated on a personal computer. Otherwise, all data analysis was carried out on an IBM 4381 computer using the Statistical Analysis System (SAS) software package (SAS Institute Inc., 1985). The significance level was $p<0.05$ for all analyses.

RESULTS

Monthly Samples

A total of 625 females between 18-53 mm SL was collected from April through September 1983 in Ditch III, and 160 of those were carrying mature eggs or embryos (Ovary Condition 3; Table 1). Fertility, as measured by percent Condition 3 females, declined sharply in July, and remained low through September. The average SL of Condition 3 females was lowest in April, followed by July, June, May, September, and August; this same rank order occurred in mean brood size. The relationship between total propagules and female SL was positive and highly significant for all months (Table 1), and comparison among the calculated regression lines showed no statistically significant differences between months (drop sum of squares, $F=1.23$; $df=11,148$; $p>0.05$). Although fewer females were reproducing in the later months, they were usually larger and carried more young.

Field Experiment

Ten collections were made for the field experiment from Ditches I and II: one from each ditch in June, before partitioning and feeding; one from the feeding and control area of each ditch in August, immediately after food supplementation ended; and one from the feeding area and control area of each ditch in September, 6 weeks after feeding was terminated. A total of 454 females 30-45 mm SL was examined. Summary statistics are given in Table 2. Mean SL of the females was significantly different between the two ditches (two-way ANOVA, $F=94.91$; $df=1,444$;

TABLE 1. Summary statistics for females collected from the Badge Station field study site Ditch III during April - September 1983. Means are ± 1 standard deviation.

	All Females		Ovary Condition			Condition 3 Females					
								Size Specific Fecundity Estimate			
Date	N	$\bar{x}$ SL(mm)	1 N(%)	2 N(%)	3 N(%)	$\bar{x}$ SL(mm)	$\bar{x}$ Brood Size	r	slope	intercept	p(F)
Apr.	103	29.2 ± 5.5	0	68(66)	35(34)	31.2 ± 5.5	9.1 ± 6.0	.92	1.01	-22.33	.0001
May	109	31.8 ± 6.4	0	67(61)	42(39)	35.3 ± 5.7	11.5 ± 6.5	.83	0.93	-21.53	.0001
June	102	29.2 ± 9.2	29(28)	20(20)	53(52)	35.0 ± 5.8	11.0 ± 5.8	.81	0.81	-17.45	.0001
July	111	24.0 ± 7.5	56(50)	51(46)	4(4)	34.8 ± 7.2	10.3 ± 5.0	.99	0.68	-13.59	.007
Aug.	100	26.0 ± 8.3	75(75)	8(8)	17(17)	39.2 ± 7.0	16.2 ± 7.7	.85	0.94	-20.81	.0001
Sep.	100	26.8 ± 6.5	86(86)	5(5)	9(9)	38.1 ± 5.7	15.8 ±10.1	.75	1.33	-34.95	.019

TABLE 2. Summary statistics for females collected in the food supplementation experiment at Badge Station during June - September 1983. Brood size is adjusted for female standard length and is ± 1 standard error. All other means are ± 1 standard deviation. * denotes a significant difference.

Ditch	Date and Treatment	n	Ovary Condition 1 n(%)	2 n(%)	3 n(%)	Condition 3 Females $\bar{x}$ SL (mm)	$\bar{x}$ Dry Weight (mg)	$\bar{x}$ Condition $(mg/mm^3)x10^{-3}$	$\bar{x}$ Adjusted Brood Size
I	June	38	0	12(32)	26(68)	33.5 ± 2.7	239.7 ± 81.5	5.9* ± 0.5	11.2 ± 0.6
I	Aug. Feeding	34	0	7(21)	27(79)	33.1 ± 2.6	252.4 ± 55.1	6.5* ± 0.4	12.2 ± 0.6
I	Aug. Control	50	0	17(34)	33(66)	36.3* ± 3.9	309.1 ± 120.7	6.1 ± 0.5	10.6 ± 0.6
I	Sep. Feeding	33	24(73)	2(6)	7(21)	32.5* ± 1.5	218.0 ± 39.6	6.5 ± 0.8	11.6 ± 1.2
I	Sep. Control	50	13(26)	19(38)	18(36)	35.4 ± 2.3	288.0 ± 60.3	6.3 ± 0.6	10.0 ± 0.7
II	June	50	0	13(26)	37(74)	37.8 ± 4.2	421.4 ± 130.4	6.5 ± 0.6	13.2 ± 0.7
II	Aug. Feeding	50	0	19(38)	31(62)	38.7 ± 3.8	433.1 ± 122.3	6.9 ± 0.5	14.3 ± 0.8
II	Aug. Control	50	0	29(58)	21(42)	37.6 ± 3.4	398.1 ± 95.1	6.7 ± 0.7	13.5 ± 1.0
II	Sep. Feeding	49	12(24)	14(29)	23(47)	37.3 ± 3.4	337.0 ± 111.4	5.9 ± 0.7	14.3 ± 0.9
II	Sep. Control	50	9(18)	11(22)	30(60)	35.7 ± 3.9	260.3* ± 95.0	5.3* ± 0.4	17.5* ± 0.9

$p<0.0001$), and because SL was highly correlated with fecundity (Table 1), the data from the two ditches were analyzed separately.

Ditch 1. The percent of nonpregnant (Ovary Conditions 1 and 2) to pregnant (Ovary Condition 3) females was compared with Chi-square analysis, and there was a significant difference when all five samples were included in the model ($X^2=35.7$; $df=4$; $p<0.0001$) (Table 2). The June, August feeding, and August control samples were not significantly different from one another ($X^2=1.8$; $df=2$; $p=0.39$), and there was no difference between the September feeding and control areas ($X^2=2.07$; $df=1$; $p=0.15$). However, there was a significant reduction in the percent of pregnant females in the feeding and control areas in September as compared to June and August ($X^2=32.4$; $df=1$; $p<0.0001$).

The mean SL of Condition 3 females ranged from 32.5 mm in the September feeding area to 36.3 mm in the August control area (Table 2). There was a significant difference between the five samples (one-way ANOVA, $F=6.36$; $df=4,106$; $p<0.0001$), and Scheffe's multicomparison test showed that only the extremes were different. Female dry weight also differed significantly between samples (one-way ANOVA, $F=3.17$; $df=4,83$; $p=0.018$), but Scheffe's test failed to reveal which samples were distinct. Somatic condition was not homogeneous between treatments (one-way ANOVA, $F=3.32$; $df=4,83$; $p=0.014$), and Scheffe's test showed that the difference occurred only between the extremes (June and August feeding).

Linear regression of brood size on female SL showed that the two variables were correlated ($F=16.6$; $df=5,105$; $p<0.0001$; $r=0.66$), and the lines generated for the five samples were not significantly different from one another (drop sum of squares, $F=0.965$; $df=9,101$; $p>0.05$).

Brood size was adjusted for female SL with analysis of covariance (ANCOVA). The difference between the adjusted brood sizes of the samples was marginally significant ($F=3.56$; $df=1,105$; $p=0.062$), with the two feeding samples having slightly larger brood sizes than corresponding control samples.

Ditch II. The relationship between the treatments and percent pregnancy in Ditch II was not as clear as in Ditch I (Table 2). Chi-square analysis for the five samples showed a highly significant difference among the treatments ($X^2=13.2$; $df=4$; $p<0.0001$). The June and August feeding samples were different from the August control sample ($X^2=10.8$; $df=2$; $p<0.0004$), and there was no difference between the August control and either September sample ($X^2=3.5$; $df=2$; $p=0.178$). There was not a significant reduction in the proportion of reproductive females between August and September as was seen in Ditch I ($X^2=5.7$; $df=3$; $p=0.124$).

The SL of Condition 3 females was marginally significant among samples (one-way ANOVA, $F=2.37$; $df=4,137$; $p<0.055$), but Scheffe's test revealed no difference between the treatments (Table 2). There were significant differences in dry weight (one-way ANOVA, $F=8.22$; $df=4,95$; $p<0.0001$) and condition (one-way ANOVA, $F=24.85$; $df=4,95$; $p<0.0001$) of the Ditch II samples. In both cases, Scheffe's test showed that the difference was in the September control sample. This sample also had significantly more young than any other group (ANCOVA, $F=18.17$; $df=5$, 136; $p<0.0001$).

Laboratory Experiment

Data pertaining to the effect of ration level on female somatic condition and growth are given in Table 3. There was no significant difference in SL between ration levels at the beginning of the experiment (repeated measures ANOVA, $F=0.12$; $df=2,35$; $p=0.889$) or after the birth of the field brood (repeated measures ANOVA, $F=0.01$; $df=2,35$; $p=0.990$), but SL was significant after the birth of the lab brood (repeated measures ANOVA, $F=15.16$; $df=2,35$; $p<0.0001$). This same pattern of significance was seen with female weight and condition factor. Scheffe's test confirmed that all three ration levels differed from one another for SL, weight, and condition. Growth in length during the interbrood interval between the field and lab broods was highly significant (repeated measures ANOVA, $F=70.44$; $df=2,35$; $p<0.0001$), as was the growth in weight (repeated measures ANOVA, $F=64.34$; $df=2,35$; $p<0.0001$). Although fish at every ration level grew, low ration fish grew slowest, high ration fish grew fastest, and average ration fish were intermediate (Figure 2).

Summary statistics for the reproductive parameters of the 39 females are given in Table 4. The interbrood intervals were not normally distributed and a nonparametric analysis (Kruskal-Wallis) was used. The comparison among rations was marginally significant (X^2 approximation= 5.7; $df=2$; $p=0.058$), but there was no clear trend in the data.

A repeated measures ANOVA showed significant differences in the number of young produced at each ration level ($F=7.85$; $df=2,35$; $p<0.001$) and in the number of young produced in the field and lab broods, independent of ration ($F=91.97$; $df=1,35$; $p<0.0001$). There was also significant interaction between ration level and brood ($F=7.17$; $df=2,35$; $p<0.003$).

TABLE 3. Summary statistics for female somatic condition and growth in the laboratory experiment. * indicates significant difference from the other two rations. Means are ± 1 standard deviation. Numbers in parentheses are sample sizes.

Ration Level	$\bar{x}$ Standard Length (mm)			$\bar{x}$ Wet Weight (g)			$\bar{x}$ Condition (mg/mm^3) x 10^{-5}			$\bar{x}$ Growth x 10^{-3}	
	Beginning	Post Field Brood	Post Lab Brood	Beginning	Post Field Brood	Post Lab Brood	Beginning	Post Field Brood	Post Lab Brood	Length (mm)	Weight (g)
Low	31.8 ± 1.5 (13)	32.2 ± 1.9 (13)	33.0* ± 1.6 (12)	0.98 ± 0.12 (13)	0.91 ± 0.18 (13)	0.94* ± 0.16 (12)	3.03 ± 0.16 (13)	2.68 ± 0.13 (13)	2.59* ± 0.20 (12)	0.53* ± 0.37 (12)	0.41* ± 2.44 (12)
Average	31.9 ± 1.2 (13)	32.4 ± 1.5 (13)	34.9* ± 1.9 (13)	0.98 ± 0.10 (13)	0.93 ± 0.13 (13)	1.21* ± 0.21 (13)	3.02 ± 0.20 (13)	2.71 ± 0.19 (13)	2.82* ± 0.16 (12)	2.44* ± 0.68 (13)	8.67* ± 1.73 (13)
High	31.8 ± 1.3 (13)	32.4 ± 1.5 (13)	36.6* ± 1.3 (12)	0.97 ± 0.13 (13)	0.93 ± 0.16 (13)	1.50* ± 0.18 (12)	3.01 ± 0.19 (13)	2.73 ± 0.17 (13)	3.05* ± 0.17 (12)	3.51* ± 0.76 (13)	14.04* ± 4.25 (12)

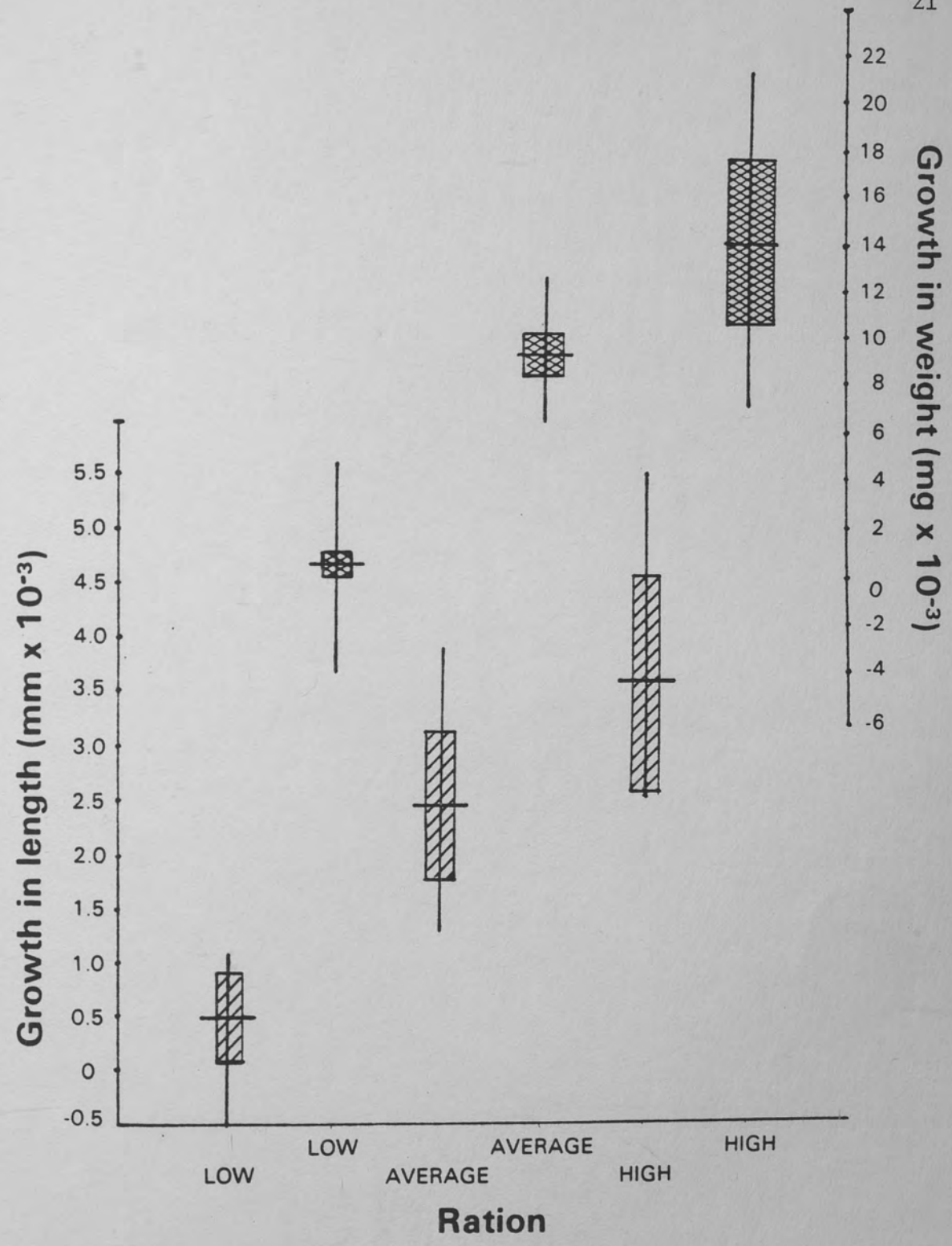

FIGURE 2. Growth in length (diagonal lines) and growth in weight (cross-hatching) for laboratory experiment females. Horizontal lines represent means; vertical lines are ranges; boxes are + 1 standard deviation from the mean.

TABLE 4. Summary statistics for reproductive variables in the laboratory experiment. Means are adjusted for female standard length and are ± 1 standard error. Numbers in parentheses are number of broods examined. *B denotes a significant difference between the field and lab broods within ration; *R denotes a significant difference between ration levels within broods.

Ration Level	Inter-brood Interval (days)	$\bar{x}$ Adjusted Total Propagules		$\bar{x}$ Adjusted Weight of Individual Young (mg)		$\bar{x}$ Adjusted Brood Weight (mg)	
		Field Brood	Lab Brood	Field Brood	Lab Brood	Field Brood	Lab Brood
Low	34 ± 7 (12)	12.2 ± 2.2 (13)	16.2 ± 1.6 (12)	16.1*B ± 0.9 (13)	8.5*B ± 0.7 (12)	181.3 ± 23.6 (13)	139.0 ± 17.5 (12)
Average	31 ± 2 (13)	12.1 ± 2.3 (13)	18.0 ± 2.2 (13)	16.3*B ± 0.9 (13)	9.5*B ± 1.0 (13)	175.7 ± 24.2 (13)	163.6 ± 24.9 (13)
High	36 ± 12 (12)	13.9 ± 2.3 (13)	20.7 ± 4.5 (12)	15.0 ± 1.0 (13)	11.4*R ± 2.0 (12)	198.9 ± 24.8 (13)	241.7*R ± 49.5 (12)
All Rations		12.7*B ± 2.0 (39)	18.3*B ± 1.9 (37)	15.8*B ± 0.8 (39)	9.8*B ± 0.8 (37)	185.3 ± 21.1 (39)	181.4 ± 21.1 (37)

There was no difference between rations for total young produced in the field broods (one-way ANOVA, $F=0.80$; $df=2,35$; $p=0.458$), but there was a difference in the lab broods (one-way ANOVA, $F=9.93$; $df=2,35$; $p<0.0004$), with fish on higher rations producing more young. However, when SL was included as a covariate, the number of young in the lab brood was no longer significantly different between the three rations (ANCOVA, $F=1.37$; $df=2,34$; $p=0.268$). SL also accounted for much of the difference between the number of young produced in the field and lab broods, but the difference across all rations was still significant (ANCOVA, $F=4.48$; $df=1,34$; $p=0.042$).

The average weight of an individual young was not significant between ration levels (repeated measures ANOVA, $F=0.78$; $df=2,34$; $p=0.468$), but was significant between the field and lab broods (repeated measures ANOVA, $F=183.15$; $df=1,34$; $p<0.0001$) (Table 4). The young in the field broods were larger than those in the lab broods, regardless of ration. There was significant interaction between ration and brood (repeated measures ANOVA, $F=5.87$; $df=2,34$; $p=0.007$). Regression of neonate weight on female SL was not significant for the field broods ($F=0.63$; $df=1,37$; $p=0.431$; $r=0.13$), but was significant for the lab broods ($F=14.93$; $df=1,35$; $p<0.001$; $r=0.55$), with larger females producing larger young (Figure 3). When the size of young was adjusted for female SL, it was found that females on low and average rations produced significantly smaller young in the lab broods (adjusted least squares means; low ration, $p<0.0001$; average ration, $p<0.0005$), while there was not a significant difference between the field and lab broods of high ration females (adjusted least squares means; $p=0.193$). The standard deviations

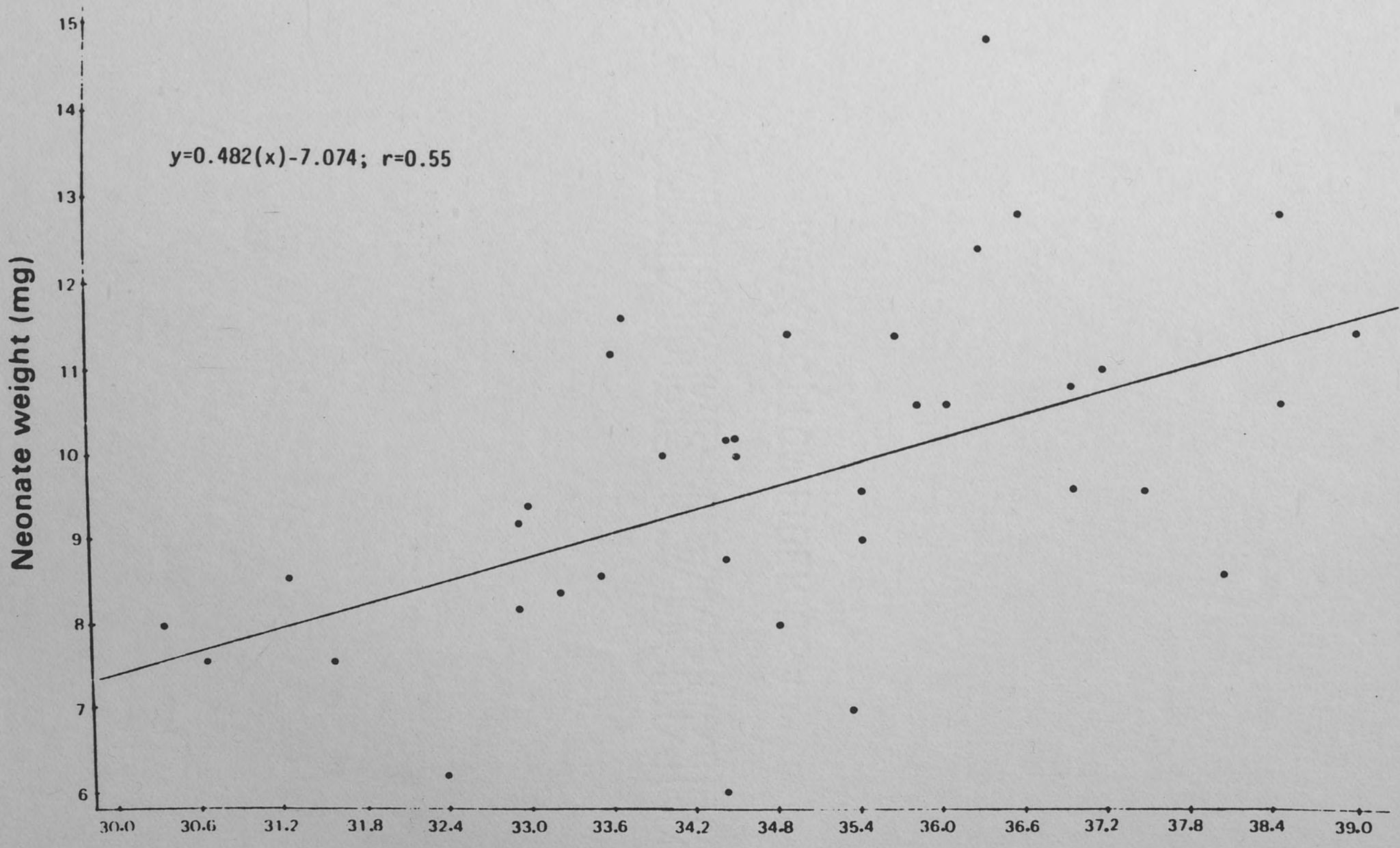

FIGURE 3. Regression of neonate weight on female standard length in the lab broods in the laboratory experiment.

of the weights of individual young within a brood were found to be the same for all ration levels (repeated measures ANOVA, $F=2.12$; $df=2,34$; $p=0.135$).

Weights of entire broods were analyzed with a nested two-way ANOVA, by ration and brood number. Lab brood weights were significantly different between rations ($F=22.48$; $df=2,34$; $p<0.0001$), with high ration fish producing heavier broods (Table 4). Even after brood weight was adjusted for female size, ration level was still significant (ANCOVA, $F=9.24$; $df=2,33$; $p<0.0006$). There was a significant difference in brood weight between the field and lab broods (ANOVA, $F=15.35$; $df=1,34$; $p<0.0004$), and adjusting for female SL did not negate the difference (ANCOVA, $F=5.44$; $df=1,34$; $p=0.026$). However, the ANOVA and ANCOVA failed to account for the growth in female SL between the field and lab broods, and the adjusted least squares means for brood weights were not significantly different from one another ($p=0.925$) (Table 4). The interaction between ration and brood was not significant (ANCOVA, $F=1.03$; $df=2,33$; $p=0.370$).

DISCUSSION

In the laboratory feeding experiment, ration level had its greatest effect on somatic characteristics of the females. Fish on high ration were longer, heavier, and in better condition than those on average or low rations at the time the lab brood was born. They also had the greatest growth in length and weight during the course of the experiment. The supplemental energy supplied to the high ration fish was invested in their soma, thereby increasing their future reproductive value (Fisher, 1930; Calow, 1979). Low ration fish also grew in length and weight but much less than high or average ration fish. A few of the low ration fish actually lost weight. Negative values in growth in length are assumed to be due to measuring error. Apparently, once the physiological commitment to brood production was made, the fish had to sacrifice somatic tissue to maintain reproduction. Average ration fish fell between the two extremes in size, condition, and growth.

The experimental fish seemed to be incapable of converting ingested food directly into young. Although it appeared that high ration fish had more young than average ration fish, and average more than low, the number of young produced could largely be accounted for by the size of the female. Fish of equal length at each ration level produced approximately the same number of young. This rigid strategy might seem confining for fish living in good environmental conditions, but is advantageous in that bad conditions are not immediately manifested as reproductive failure.

Ration level had no direct effect on the weight of individual young, and females of equal size produced young of equal size. As with number of young produced, much of the variation in the weight of young could be attributed to the length of the female. I hypothesized that females might partition energy differentially within a brood, with females on low ration producing a few large young and a few small young. However, this was not the case. Once the energetic commitment was made, all young in a brood developed at the same rate and were born at approximately the same size. This implies that all eggs had about the same energy content at the time of fertilization.

The number of days between broods was not influenced by ration level. There was an unexpected tendency for high ration females to have longer interbrood intervals, but the differences were not significant. If the experiment had been successfully carried out through another brood, the stressed females might have been unable to produce the next batch of eggs as quickly as females in better condition. At that point, the interbrood intervals might have more accurately reflected ration level, as suggested by Snelson et al. (1986).

The field experiment demonstrated that a mid-summer slump in reproduction does occur in some east-central Florida molly populations. However, the results did not confirm Wetherington's (1982) idea that the decreased reproduction is caused by habitat limitation leading to food shortage. This lack of significant results in the field could have several causes. The reproductive slump might have been due to environmental cues other than food availability. If the fish were not food-limited, supplementing their diet would have no effect. A second

possibility is that the level of food supplementation was insufficient to make a difference. Competing species, such as the abundant Gambusia affinis, had equal access to the food and may have gleaned most of the supplementation. A third possibility is suggested by the results of the lab experiment. If the food supplementation had any effect, it would have been on the somatic characteristics of the females, not on the number of young they produced. An experiment designed to measure the growth of individual females would be a more appropriate way to assess the effect of food supplementation in the field.

How might a life history strategy that involves putting excess energy into the soma instead of directly into reproduction have evolved? If the organism has a good chance of reproducing many times, it might benefit by having a larger body that could produce more young. Future fecundity would outweigh immediate reproductive gains. This strategy has been suggested for several long-lived, iteroparous species (Wilbur et al., 1974; Nichols et al., 1976; Mann and Mills, 1979). A molly that lives in central Florida for two years has the capability of producing fourteen broods in her lifetime. These fish could increase their overall fecundity by growing, especially if growth occurred during the first reproductive season.

Another explanation for the molly's strategy is that growth is a secondary effect of ration level caused by the opportunity to store energy that will be harvested later. Apparently, the energy for vitellogenesis normally comes from something other than ingested food or the female's structural body tissue. Stored energy, such as lipid, is a likely candidate for this source. Lipids are high in caloric value,

stable, and easily deposited (Shulman, 1974), and lipids are more energy-rich than proteins or carbohydrates (Philips and Brockway, 1959). They are the major form of energy storage in organisms with high metabolic requirements, such as insects, birds, and fish (Shulman, 1974). An excellent strategy for an iteroparous, ovoviviparous fish living in a seasonally fluctuating environment would be to store energy when resources permit. Regardless of future resource conditions, reproduction at a constant rate could continue, supported, at least for a while, by stored energy. The mid-summer reproductive slump could be a reflection of depleted lipid stores caused by the heavy demands of spring reproduction. Research is currently underway to determine if there is a lipid cycle in mollies and how it may relate to the reproductive cycle.

An unexpected result of the lab experiment was the difference between the field and lab broods. Across all rations, the lab broods were larger, but had significantly smaller young than the field broods (Table 4). This disparity may have resulted from some seasonal cycle in the source population. Field broods from females collected at a different time might have been larger with smaller young than the subsequent broods, or the brood and neonate sizes could change steadily throughout the season. Another possibility is that the difference between the broods was strictly a laboratory artifact caused by something other than ration level. It is interesting that in the period of one reproductive cycle, the females could increase brood size nearly 70%. The young in the lab broods appeared to be healthy, and there was no reason to suspect that they were premature or otherwise abnormal, or that they would not have survived in nature. Smith and Fretwell (1974)

argued that life history parameters, such as size of brood or young, should evolve toward an optimum value. Other studies (Capinera, 1979; Crump, 1981; Kaplan and Cooper, 1984; Meffe, pers. comm.) suggest that selection for variation in these tactics is advantageous, especially in fluctuating environments. The data in Table 5 demonstrate that there is much variation in brood and propagule sizes both within and between related species of poeciliids. The ability of female mollies to produce such a range in size of broods and young as observed in this study represents a great plasticity in two important reproductive parameters. If this variability is correlated with some environmental cue, plasticity could be an important component in determining the sailfin molly's life history strategy.

TABLE 5. Brood and propagule size for species of poeciliid fishes. s.d. = standard deviation; C.V. (%) = coefficient of variation; s.e. = standard error; C.I. = confidence interval.

Study	Brood Size	Propagule Size
Hester, 1964 *Poecilia reticulata*	range - 8-21	neonate length(mm) - $\bar{x}$=6.08 ±1.06(s.d.)
Constanz, 1974 *Poeciliopsis occidentalis*		egg weight(mg) - site 1 - $\bar{x}$=1.82, C.V.(%) 34.25 site 2 - $\bar{x}$=2.09, C.V.(%) 33.54 embryo weight(mg) - site 1 - $\bar{x}$=2.81, C.V.(%) 60.55 site 2 - $\bar{x}$=2.76, C.V.(%) 59.80
Thibault & Schultz, 1978		
Poeciliopsis monacha	$\bar{x}$=11.8 ±0.96(s.d.)	neonate length(mm) range - 7.2 - 8.9
P. lucida	11.0 ±0.67	4.7 - 8.8
P. prolifica	4.0 ±0.32	6.5 - 8.0
P. turneri	3.6 ±0.29	12.0 - 17.0
Poecilia reticulata	24.2 ±1.07	6.0 - 7.5
Constanz, 1979 *Poeciliopsis occidentalis*	site 1 $\bar{x}$=4.7 ±1.1(s.e.) site 2 13.6 ±2.5	egg weight(mg) - site 1 - $\bar{x}$=2.15 ±0.14(2s.e.) site 2 - 1.64 ±0.09
Dahlgren, 1979 *Poecilia reticulata*	range of $\bar{x}$=10.7 ±5.7(s.d.) to 18.2 ±12.7	embryo length(mm) range of $\bar{x}$=3.6 ±2.3(s.d.) to 5.8 ±2.4
Snelson, 1982 *Poecilia latipinna*		neonate length(mm) - $\bar{x}$=8.65, range(mm) = 8.3-9.1
Stearns, 1983 *Gambusia affinis*	range of $\bar{x}$=16.6 ±10.4 to 30.2 ±9.1(95%C.I.)	neonate weight(mg) - range of $\bar{x}$=0.96 ±0.03 to 1.19 ±0.06(95%C.I.)
Turner & Snelson, 1984 *Belonex belizanus*	$\bar{x}$=99.4 ±5.7(s.e.) range = 6-322	neonate length(mm) - range - 14.3-17.7 neonate weight(mg) - range - 5.7- 7.8
Meffe, pers. comm. *Gambusia affinis*		wild embryo weight(mg) - range - 0.6-2.2 lab embryo weight(mg) - range - 1.1-1.5

APPENDIX TABLE 1. Physical parameters for the Badge Station field experiment site taken from 16 April - 14 September, 1983. The highest water level was recorded as "0" and other depths reported as "cm below 0."

Date	Fish Sample Taken	Water Surface Temperature (C)	Salinity (ppt)	Depth (cm below 0)
16 Apr.	yes-monthly	31	7	n/a
15 May	yes-monthly	39	13	20
22 May	no	31	20	12
3 June	no	30	19	13
14 June	yes-experimental, monthly	33	12	0
16 June	no	32	13	n/a
19 June	no	29	13	n/a
26 June	no	31	12	2
3 July	no	30	12	12
10 July	no	29	11	13
17 July	yes-monthly	31	13	n/a
23 July	no	31	15	19
31 July	no	30	15	11
2 Aug.	yes-experimental	30	11	4
16 Aug.	yes-monthly	34	9	11
30 Aug.	no	37	6	6
14 Sep.	yes-experimental, monthly	30	10	9
		$\bar{x}$ = 31.6 range = 29-39	$\bar{x}$ = 12.4 range = 6-20	$\bar{x}$ = 11 range = 2-20

APPENDIX TABLE 2. Total propagules, normal young, and abnormal young in the field brood, lab brood 1, and lab brood 2 of the laboratory experiment. There were no abnormal young in any field brood and there were no unfertilized eggs in any brood. Numbers in parentheses are total number of broods examined.

Ration	Field Brood		Lab Brood 1				Lab Brood 2			
	Total Young	Broods with Abnormal Young	Total Young	Normal Young	Abnormal Young	Broods with Abnormal Young	Total Young	Normal Young	Abnormal Young	Broods with Abnormal Young
Low	128	0 (13)	180	180	0	0 (12)	96	82	14	3 (10)
Average	125	0 (13)	266	265	1	1 (13)	274	213	61	8 (13)
High	148	0 (13)	345	344	1	1 (13)	296	59	237	10 (11)

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