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THE INFLUENCE OF SOMATIC INVESTMENT ON THE PATTERN
OF REPRODUCTION IN POECILIA LATIPINNA (PISCES: POECILIIDAE)

BY

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THESIS

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ABSTRACT

In Poecilia latipinna size-specific reproductive and survivorship
patterns were correlated with changes in habitat availability. Of the
numerous physical, chemical, and biological parameters associated with
a reduction in available habitat, probably the most important was
reduced food availability. Large (old) females, theoretically with a
low reproductive value, allocated energy to reproduction regardless of
habitat and, presumably, food availability. When reproductive
activities were initiated in March, habitat availability was modest.
In association with a severe reduction in available habitat in April,
large females were subject to a substantial loss of body weight during
the yolk-loading phase of the reproductive cycle. This loss, primarily
of somatic tissue, was very costly and heavy mortality ensued. Habitat
availability increased during late May and June and survivorship
increased. By August the somatic condition of large females had
improved significantly. As in April, yolk-loading resulted in a loss
of body weight; however, the loss consisted of approximately 70% lipid.
Although the cost was lower than April, the necessity of subsidizing
reproduction with somatic tissue may account for the slight reduction
in survivorship observed in September. Smaller (younger) females,
theoretically with a higher reproductive value, allocated energy to
reproduction in response to increases in habitat, and presumably food
availability. This response was in the form of an increased number of

small reproducing females and was not evident until the month following the increase in available habitat. In contrast to large females, reproductive activities among small females were initiated in April. In association with a severe reduction in habitat availability, small females were subject to a loss of dry weight during yolk-loading, which consisted of approximately 44% lipid. The cost of reproduction was reduced and survivorship improved relative to the large females. Despite an increase in available habitat in June, small females curtailed reproduction in favor of survival and increased fecundity afforded by a greater body size. By early August an increase in reproductive activities was evident among small females. The somatic condition of these females was significantly improved in comparison to April females. In contrast to large August females, small females did not subsidize reproduction with somatic tissue. The change in body weight was attributable to a loss of lipid. By early September the available habitat had increased dramatically. In comparison to August, the high number of small reproducing females suggested the response to improved conditions may be rapid.

Changes in food availability and, thus the total energy budget (lower in spring, higher in the summer and fall) and the associated cost of reproduction (higher in spring, lower in fall) from April to September were not reflected by changes in fecundity. It appeared that under the conditions that prevailed during this study, a female that made a commitment to reproduction produced a size-specific brood of a fixed quality regardless of food availability and reproduction cost. If a female was able to assimilate excess energy during the gestation period, that energy was allocated in maintenance (i.e. repaying any

somatic debt) and growth.

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INTRODUCTION

The life history of an iteroparous organism may be viewed as a dynamic interdependence between three basic biological processes, growth, maintenance, and reproduction. All organisms live in a finite environment and, consequently, have limited resources of time and energy at their disposal. Reproduction at any given time is associated with a cost that must be paid in terms of subsequent survival of the parent and its future reproductive success. Therefore, it is critical that resources be optimally allocated among these three basic processes, particularly during periods of resource limitations (Pianka, 1976; Calow, 1979).

What determines the optimal allocation of net energy into reproductive vs. non-reproductive (somatic) tissues and/or activities? Somatic tissues are important in the acquisition of matter and energy. However, an organism's soma is of no selective value unless it enhances life-long reproductive success. Consequently, allocation of net energy is a function of the balance between an organism's current and future reproductive value. There is a negative causal relationship between the time and energy that an individual invests during a current act of reproduction and the individual's survivorship and expectation of future offspring (Fisher, 1930; Hamilton, 1966; Williams, 1966; Emlen, 1970; Taylor et al., 1974; Schaffer, 1974; Pianka and Parker, 1975; Pianka, 1976). Thus, an individual with a high probability of future reproductive success should be more hesitant to risk its soma in present

reproductive activities than an older individual with both a lower probability of survivorship and a lower expectation of future offspring (Williams, 1966; Gadgil and Bossert, 1970; Schaffer, 1974; Pianka and Parker, 1975; Giesel, 1976; Pianka, 1976).

This prediction becomes more complex for organisms with indeterminate growth. Among such species fecundity is usually positively correlated with body size (e.g. Svardson, 1949; Scott, 1962; Hester, 1964; Bagenal, 1969; Tinkle, 1969; Tinkle and Hadley, 1973; Avery, 1975; Wootton and Evans, 1976; Constantz, 1979). A reduction in growth rate due to an individual directing matter and energy into reproduction will lower its expectation of future offspring, since it will reduce the size attained at future breeding periods (Lawlor, 1976; Calow, 1973, 1979). The "decision" not to reproduce, resulting in the diversion of matter and energy into increased growth and survivorship, should be based upon the expectation of future offspring. Consequently, an organism with a low expectation of future offspring should commit energy to reproduction rather than growth. For such individuals there is less enhancement of fitness associated with increasing body size and more value to be gained from immediate reproduction. Under this principle of allocation, age-specific growth and fecundity rates should be adjusted by natural selection so that a female maximizes her life-long genetic contribution to future generations. Lifespan will ultimately be the product of the specific adjustment that is reached (Gadgil and Bossert, 1970; Snell and King, 1977; Calow, 1979). This adjustment will define an organism's life history tactic (reviews by Pianka, 1976; and Stearns, 1976, 1980).

Through our studies of the reproductive ecology of the sailfin molly _Poecilia latipinna_ (Pisces; Poeciliidae), we became interested in its life-history tactics, especially the survival of reproducing females as a function of the cost of reproduction. There are at least two ways by which this cost might be formulated (Calow, 1979); (1) directly, by measuring the correlation between current reproduction and future reproduction, survival, and growth under defined conditions (Snell and King, 1977; Law, 1979; Browne, 1982; Tallamy and Denno, 1982), or (2) indirectly, through an understanding of the causal basis of this correlation (Langer, 1956; Bocher and Larsen, 1958; Tinkle, 1969; Harper and Ogden, 1970; Harper, 1977; Rickleffs, 1977).

This study will employ the latter approach. The age-specific pattern of growth, reproduction and survival will be elucidated from 13 monthly samples. In conjunction with two of these samples, the somatic investment to reproduction by large and small females will be determined. The cost of this investment will be assessed in terms of its impact on the age-specific pattern of growth, reproduction, and survival.

MATERIALS AND METHODS

Study Species. The sailfin molly is ubiquitous in coastal environments from South Carolina to the Yucatan Peninsula of Mexico (Rosen and Bailey, 1963). Females are ovoviviparous and produce live young at intervals of approximately 30 days (Snelson and Wetherington, 1980). During the time a brood of embryos is developing in the ovary, the ova of the succeeding brood remain small and undifferentiated. Following parturition, vitellogenesis progresses quickly so that the ova of the next brood mature and are ready for fertilization in 2-7 days ("Gambusia type" following Turner, 1937). The yolk supply appears adequate to sustain the developing embryos during the period of gestation and the ovarian follicle in which the embryo is retained during development shows no specialization for maternal-embryo nutrient exchange (Turner, 1940; Amoroso, 1960). Consequently, the majority of the energy required for a single act of reproduction must be made available during the 2-7 day yolk-loading period between the birth of one brood and the fertilization of the next. Since successive broods rarely overlap (Turner, 1937, 1940; Scrimshaw, 1944; Hubbs, 1964), an estimate of the relative cost of reproduction can be made through a comparison of the somatic condition of females that have just given birth with that of females carrying recently fertilized eggs.

Study Site. Field studies were conducted on the east coast of central Florida at Merritt Island, Brevard County. Aquatic habitats

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on Merritt Island consist primarily of shallow mosquito control
impoundments surrounded by earthern levees and dredged ditch systems.
The study site was an ca 3-ha impoundment 2 km WNW of the Vehicle
Assembly Building at the John F. Kennedy Space Center (T22S; R36E;
Sec. 12). The water was generally shallow, averaging less than 0.5 m.
Marginal areas were densely vegetated with a variety of submerged and
emergent aquatic plants. The central portion supported submerged
stands of muskgrass (Chara sp.) that was especially dense during the
fall. Deep water was confined to a dredged canal which communicated
freely with shallow marginal areas. This canal averaged approximately
2 m in depth and was relatively free of rooted aquatic vegetation.
This site is the TOWY study site of Snelson (1980).

During the 13 months of study, salinity varied from 2.5 to 12.0
ppt ($\bar{x}$ = 5.2). Water temperatures, monitored continuously at an
adjacent similar site, ranged from 12 to 21°C ($\bar{x}$ = 18) during the
winter and from 21 to 31°C ($\bar{x}$ = 29) in the spring and summer. Water
depth and habitat availability underwent dramatic fluctuations in
response to the annual rainfall cycle. A more detailed environmental
analysis of this site was given by Snelson (1980).

Field Studies. Field sampling began in November 1976 and
continued through November 1977. Fish samples were taken near the
first of each month with a seine 3.7 m long and 1.2 m deep with 4.8 mm
mesh. All fish caught were preserved in 10% formalin and later
transferred to 45% isopropyl alcohol. A conscious effort was made to
sample all habitats and to sample the same general areas each month.
The study fish consisted of a random subsample of about 150 mature

females removed from each monthly collection. The criterion for maturity was a standard length (SL) equal to or exceeding 18 mm, the size of the smallest pregnant female recorded during five years of study on several east Florida populations of P. latipinna (Snelson, 1980). All females in a subsample were measured to the nearest 0.1 mm SL and their ovaries removed. On the basis of ovarian development, females were assigned to one of three reproductive conditions: (1) with undeveloped ovaries; (2) with developing ova; or (3) with mature fertilized eggs or developing embryos (pregnant). Mature eggs or developing embryos were counted in all pregnant females.

Water level was monitored monthly in conjunction with fish sampling. A piece of heavy plastic pipe was driven into the substrate in the deepest location in the study site. The distance from the top of the pipe to the water surface was recorded monthly. The highest water level recorded during the study (September, 1977) was considered the zero level and all other monthly values were expressed in cm below zero. Concurrently with water level measurements, photographs were taken from several fixed positions around the impoundment. From these photographs, habitat availability, measured by the degree of inundation of shallow marginal areas, was visually estimated. The conditions in September 1977 were considered maximum availability (100%) and conditions in other months were expressed as per cent decrease below maximum.

Comparisons of reproduction patterns among monthly field samples were based upon changes in the length distribution of pregnant females, per cent adult females pregnant, and brood sizes. Because there was

a significant positive correlation between brood size and female length ($p<0.05$), analysis of covariance was employed using SL as a covariate. Brood sizes were log transformed prior to analysis in order to stabilize within sample variance. The analysis was limited to females from 28 to 33 mm SL because the size ranges of reproducing females differed dramatically among monthly comparisons. This corresponded to the narrowest size range of reproducing females observed in a monthly collection (June) and usually encompassed at least 50% of the reproducing females in any collection. Because a comparison among the seven months in which there was reproduction revealed no significant differences in the relationship between brood sizes and female size ($F = 1.20$; $p<0.05$), the mean clutch size of each monthly sample was adjusted to the mean length of all pregnant females ranging from 28 to 33 mm SL ($\bar{x} = 30.6$; $n = 156$). Thus, fecundity in each monthly sample was presented by a mean adjusted brood size. A probability level of 0.05 was used in comparisons of adjusted brood sizes between months.

Laboratory Studies. Females for laboratory analysis (lab samples) were collected in mid-April and late July using a seine 15.3 long and 1.2 deep with a 4.8 mm mesh. Because the July lab sample was taken chronologically nearer to the August field sample than the July field sample, and because the July lab sample reflected the biological and ecological conditions of the August field sample, the lab sample taken in the late July is hereafter referred to as the August lab sample. Females suspected of carrying mature eggs were distinguished in the field by the presence of a darkened area (gravid spot) around the

urogenital opening; they were isolated in a styrofoam chest. Females suspected of carrying term embryos were identified by a visibly swollen abdomen; they were placed in individual one-liter jars containing collection site water. Both groups of females were held alive in the laboratory for 72 hours to allow for evacuation of the gut.

Females suspected of carrying term embryos were subsequently checked every four hours. When a brood was found, both the female and her progeny were sacrificed. The female was measured to the nearest 0.1 mm SL and the young were counted. The ovary of the female was removed, examined for unborn young, unfertilized eggs and maturing ova, and then discarded. The gut was checked for ingested young. The female and her brood were dried at 60°C for seven days followed by storage at 0°C.

Females suspected of carrying mature eggs were sacrificed after the holding period and measured to the nearest 0.1 mm SL. The ovary was removed and teased apart in distilled water. The clutch was considered mature if the eggs were large and uniform in size with a blastodisc present on at least one. Females with broods at earlier or later stages were discarded. If the eggs were mature, the individual ova were freed of follicular material. Eggs that ruptured during handling were counted and discarded. The diameter of the remaining eggs was determined to the nearest 0.01 mm with an ocular micrometer. Abnormal swelling due to water imbibition appeared minimal. The female and her brood were dried at 60°C for seven days followed by storage at 0°C.

In each lab sample, five of the largest and five of the smallest females of each reproductive condition were used for analysis. Small

females ranged from 24 to 28 mm SL and large females ranged from 31 to 35 mm SL. Females and their broods were dried to a constant weight, a process requiring about 30 days at 60°C followed by vacuum desiccation for 48 hours. Females were weighed to the nearest 0.01 mm using an electronic microbalance (Cahn Model 4100) and then ground to a uniform consistency using a mortar and pestle. Individual eggs and embryos were weighed to the nearest 0.01 mg. Members of each brood were pooled and ground to a uniform consistency using a mortar and pestle. Ground samples were redried at 60°C for 72 hours and then stored in a vacuum desiccator.

Caloric contents of female bodies, eggs, and young were measured with a Phillipson oxygen microbomb calorimeter (Gentry and Wiegert Company, 1969). Determinations were made of three aliquots (1-5 mg) of bodies and broods for the April sample and one aliquot (1-5 mm) for the August sample. Residues remaining after each caloric determination were ashed at 550°C for 24 hours. Results were expressed as calories per mg of ash free dry weight. Lipid content of bodies and broods were assessed using a Goldfisch fat extractor (Harowitz, 1975) with a solvent system of chloroform and methanol in a 2:1 ratio (Christie, 1973). Determinations were made of three aliquots (1-5 mg) of bodies and broods for the April sample and two aliquots (1-5 mg) for the August sample.

Analysis of variance (ANOVA) was employed for all comparisons between means. A nested one-way model was used for comparisons between means based upon replicate determinations. These included all comparisons within the April and August samples, and comparisons

between the April and August samples involving per cent lipid in
females, eggs, and young; dry weight and diameter of eggs; and dry
weight of young. The remaining comparisons employed a simple one-way
ANOVA model. Due to significant positive correlations with SL, analyses
involving either brood sizes or female dry weight were performed with
length as a covariate. Because there was no significant difference in
the relationship between female dry weight or clutch size and female
length in any comparison ($\rho < 0.05$), brood size and dry weight were
represented by means adjusted for differences in SL. Brood sizes were
log-transformed prior to analysis to stabilize within sample variance.
In the simple one-way comparisons of caloric values between months,
April females were represented by the mean of the three replicate
determinations. All results expressed as per cents were normalized
prior to analysis using an arcsin transformation. A probability level
(p) of 0.05 was employed for all statistical tests.

RESULTS

Field Studies. Water level and habitat availability underwent
dramatic fluctuations in response to the annual rainfall and evaporation
cycles (Fig. 1). Water was relatively high throughout the winter
months of 1976. The level began to drop in February and reached its
lowest point in early May, when only 50% of the impoundment was
inundated. At water depths of -40 cm and lower, the shallow, vegetated
marginal areas were exposed and fish were concentrated into the
relatively unproductive ditch that ran through the impoundment. Water
levels rose slowly throughout June as a result of early summer rain.
By early July 80% of the habitat was flooded which included limited
areas of marginal vegetation. Water levels began to recede in July due
to slackened rainfall. By August a 10% reduction in habitat
availability was evident with access to only limited areas of marginal
vegetation possible. Due to heavy rainfall in late summer, water level
increased dramatically during August and reached a peak level in
September, when all marginal areas were flooded and habitat availability
was maximum.

From November 1976 through February 1977 females were non-
reproductive (Fig. 2). Judging from the similarity of length-frequency
distributions, growth during the winter months was curtailed. The
first indications of reproductive activity were evident in March, when
females with developing ova were present (Fig. 2). The proportion of

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females with developing ova increased with increasing female length. The shape of the histogram also changed dramatically in March, as young born the previous fall (September, early October) were first recruited into the sample. Pregnant females were first collected in early April. These females had overwintered, and at least the large ones must have been reproductive the previous fall. Small females (<27 mm SL) contained primarily developing ova. By May, a substantial portion of these small females were pregnant. Greater pregnancy among small females resulted in an increase in the per cent of adult females pregnant and a decrease in the mean size of reproducing females (Fig. 3). Only the smallest females (<23 mm SL) were nonreproductive in May (Fig. 2).

The June sample was characterized by a dramatic decline in the number of reproducing adults (Figs. 2, 3). This was primarily because large females disappeared. In May 39% of the females sampled were greater than 27 mm SL and all were reproductive. By June this figure had dropped to only 12%. This comparison becomes more dramatic when the 26-27 mm size group is included. In May 67% of the females sampled were greater than 25 mm SL and all were reproductive. In June this value had declined to 17%; however, a large proportion of females in the 26-27 mm size group had curtailed reproduction (Fig. 2). Mortality or the cessation of reproduction was also evident among small females. Consequently, the June adult population was composed predominately of small nonreproduction females, many of which had over-wintered as virgins or had been born in early spring. Pregnant females, only 9 of the 155 sampled, were restricted to the larger size classes.

Depressed reproduction continued into July. As in June, only large females were reproductive (Fig. 2). Slight increases in both the per cent pregnancy and the mean size of reproducing females resulted from increased survivorship of large females coupled with growth and increased pregnancy among small females (Fig. 3). There was a 17% increase between June and July in the per cent pregnancy of females greater than 26 mm SL, and a 2 mm increase in the mean size of reproductive females.

In August, reproduction increased substantially. Many large pregnant females were present, and the initiation or resumption of reproduction by smaller adults resulted in a sharp increase in pregnancy percentages and a decrease in the mean size of pregnant females (Fig. 3). Recruitment of small females (<23 mm SL) had decreased in comparison to the two previous months, probably a reflection of the reduction in births during the June-July slump (Fig. 2).

Although recruitment and reproduction among small females increased substantially in September, increased mortality among large females resulted in a slight decrease in the per cent of adult females pregnant and a sharp decrease in the mean size of pregnant females (Fig. 3). Pregnant females less than 20 mm SL were present for the first time. Small females consisted primarily of virgins born during the spring (Fig. 2). At the end of the reproductive season in October, pregnancy was limited primarily to large females (Fig. 2). This was reflected in an increase in the mean size of reproducting females and a decrease in per cent pregnancy (Fig. 3). By early November reproduction had ceased. The size distribution of females was similar

to that of October, consisting primarily of small females.

A comparison among adjusted brood sizes from April to August revealed no significant differences despite fluctuations in the per cent of adult females gravid and the mean size of gravid females (Fig. 3). Consequently the relationship between brood size and female size for these months can be summarized by a single regression equation ($Y = -0.46 + 0.05X$, where X = SL and Y = brood size). The decline in the adjusted brood size observed in October was the only change that was significant.

Laboratory Studies. Results of the lab study are summarized in Table 1. In the April sample, small females with mature eggs had a lower adjusted dry weight, caloric value, and per cent lipid than small females with young (Table 2). The differences in caloric value and per cent lipid were statistically significant. In contrast, large females with eggs had a lower (marginally significant) adjusted dry weight, but a slightly greater caloric value and per cent lipid than large females with young. Neither of the latter two differences were significant.

As in April, small females with eggs in August had a lower adjusted dry weight, caloric value, and per cent lipid than small females with young (Table 2). Although none of these comparisons were significant, the differences in caloric value and per cent lipid were of the same magnitude as those observed for small April females (Table 1). Similarly, large females with eggs had a lower adjusted dry weight, caloric value, and per cent lipid than large females with young. Despite insignificance in these comparisons, the difference in per cent

lipid was of the same magnitude as that observed for small April females (Table 1). Lack of significance in many comparisons involving the August sample may be due in part to fewer replicate determinations per female.

The condition of females in the August sample was vastly improved from that of females in April (Table 3). Regardless of size and reproductive condition, females in August had a greater adjusted dry weight, caloric value, and per cent lipid than their counterparts in April. The differences in per cent lipid among females with eggs were the only comparisons that were not statistically significant.

Despite the significant positive correlation between female size and brood size, female size did not affect the quality of eggs or young within monthly samples. Among females with mature eggs, the only significant comparison was that of per cent lipid between April females (Table 4). Among females with young, the only significant comparison was that of per cent lipid and lipid per propagule between August females (Table 4). Uniformity among eggs and young was also reflected in between month comparisons. The only significant difference was that of per cent lipid between young of small females (Table 3).

From the original data, the relative cost of reproduction in April and August was estimated (Table 5). This analysis is based on the assumption that differences in energetic parameters between females with term young and females with mature eggs reflect relative costs imposed during the yolk-loading period. Since a comparison of egg quality between female sizes revealed only minor differences, the best estimate of the investment in reproduction was the total number of

calories in a brood. In both April and August, brood size and, hence, total brood calories was significantly and positively correlated with female size ($p<0.05$). However, a comparison between female size groups revealed that the ratio of the number of body calories lost during the yolk-loading period to total brood calories within each month was nearly identical. Thus, small females tended to allocate the same proportion of body calories to reproduction as large females. There was, however, a major difference in the relative quantities of somatic tissue and lipid catabolized to generate these body calories. Because large April females underwent very little change in body lipid, the decline in the adjusted dry weight consisted primarily of somatic tissue (Table 5). In contrast, the decline in adjusted dry weight among small April females consisted of nearly 50% lipid. In August, 70% of the decrease in adjusted dry weight among large females was attributed to a loss of lipid. Small females, on the other hand, may have gained somatic tissue; since the loss of body lipid was five times greater than the loss of adjusted dry weight. In comparison to small females, therefore, large females in both April and August used more somatic tissue to subsidize reproduction. Consequently, large females incurred a greater cost during the yolk-loading period than small females. This was especially evident among large April females. In contrast to April, large and small females in the August sample allocated fewer calories to reproduction and did not incur as great a cost.

DISCUSSION

Many authors (e.g. Williams, 1966; Cody, 1966; Charnow and Krebs, 1973; Anderson, 1978) have argued that survival and reproduction represent two alternative ways of using energy. The physiological basis for an inverse relationship between reproductive output and survival is that both activities draw resources from a limited resource pool. Reproduction is most likely to have an adverse effect on a female when materials and energy otherwise necessary for her metabolic well-being are channelled into reproductive activities ("Competitive Hypothesis" of Calow, 1979). Evidence for such competition has been reported in both plants (Harper, 1977; Sohn and Polocansky, 1977; Primack, 1979) and animals (Jones and Ward, 1976; Tyler and Dunn, 1976; Calow, 1977; Calow and Woollhead, 1977; Randolph et al., 1977; Bryant, 1979). Allocation of net energy among the competing processes of growth, maintenance, and reproduction can be strongly influenced by proximal factors such as resource availability (Spight and Emlen, 1976; Ballenger, 1977; Browne, 1978; Haukioja and Hakala, 1978; Woollhead and Calow, 1979) and various aspects of the physical environment (Beatley, 1969; Colson, 1969; Bowden, 1970; Grier, 1973; Falke and Smith, 1974). Among vertebrates, this appears to be especially true of fishes (Stearns, 1977). Consequently, treatments of reproductive ecology must consider the ability of organisms or genotypes to vary patterns of energy allocation among the competing processes of growth, maintenance

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and reproduction in response to environmental variation (Bradshaw, 1965; Giesel, 1976; Nichols, et al., 1976). Variations in patterns of energy allocation will be strongly influenced by age (Schaffer, 1974) and, for organisms that continue to grow following sexual maturity, by body size (Gadgil and Bossert, 1970).

The most variable environmental parameter measured during this study was habitat availability. Of the numerous physical, chemical and biological parameters associated with a reduction in available habitat, probably the most important was reduced food availability. Poecilia latipinna is primarily herbivorous, feeding on a combination of periphyton, detritus, and algae (Harrington and Harrington, 1961). Through the winter until early March, water levels were moderately high, giving females access to marginal vegetation. However, receding water levels in the spring and early summer reduced or entirely eliminated shallow, productive marsh areas, thus eliminating prime foraging sites. Receding water levels were also correlated with a decline in the productivity of periphytic algae (Snelson, 1980) and the standing crop of Chara sp. Thus, throughout most of the period when water level was at -40 cm or lower, mollies were crowded into the dredged ditch, where food may have been limiting. Water levels rose slowly during June and by early July were sufficient to inundate nearly 80% of the available habitat. In comparison to May, females experienced an increase in food availability. However, this increase was probably not dramatic. As in May, periphytic algae productivity remained low (Snelson, 1980). Moreover, only 5% of the inundated habitat was represented by marginal vegetation. During July habitat availability underwent a slight

decline. By early August, water had receded to a level allowing access to only very limited marginal areas. Consequently, food supply probably declined below the level of June but was not at the critically low level of May. Due to extensive rains in August, habitat availability increased dramatically. By September much of the shallow, productive marshy areas surrounding the study site were flooded. A dramatic increase in food availability was probably realized through expanded foraging areas and the release of nutrients from oxidized sediments.

Reproductive patterns at the population level appeared to be strongly influenced by changes in habitat availability. The most dramatic response was through variation in the per cent of adult females pregnant. This response was not immediate, however, but lagged behind changes in habitat availability by about a month. In the spring the consequences of this delayed response were severe. When reproduction was initiated in March, females had access to nearly 85% of the available habitat. By May habitat availability had declined to a seasonal low; yet the per cent of adult females pregnant had attained a seasonal peak. Moreover, the April lab data revealed that reproduction was very costly implying that food was limiting. It appeared as if many females had committed themselves to reproduction prior to May. This commitment may have been a function of both the prevailing environmental conditions in March and the somatic condition of females following the winter latent reproductive period. However, the importance of the latter is uncertain. Unfortunately, very few data are available pertaining to winter fattening in subtropical

cyprinodontoid fishes with cyclic reproductive patterns. During the winter months, reproduction is curtailed in many of these fishes; however, limited amounts of activity are possible. Because fecundity is highly correlated with body size, excess energy should be devoted to somatic growth. Low winter temperatures may preclude growth, necessitating the storage of excess energy in the form of fat. Fundulus similis spawned repeatedly during the year except for November, December, and January when the temperature was low and the photoperiod short. Lipid content continuously increased to a maximum during this latent period (de Vlaming, et al., 1978). The August lab data of this study on P. latipinna indicated that females stored lipid and used it during yolk-loading. Although the lipid content of winter females was not assessed, the sudden surge in growth, as well as the high percentage of reproductive females in the spring, may be a reflection of winter fattening. The continued reproduction during May in spite of deteriorating environment conditions was probably a result of the rapid and, presumably, unpredictable nature of the changes in habitat availability.

The consequences of the high cost of spring reproduction were evident in the June field sample. Shifts in the size class structure suggested mortality among reproducing females was heavy. The per cent of females pregnant also declined to a seasonal low. By early July, habitat availability had increased so that females had access to marginal vegetation. However, the per cent of pregnant females in July had increased very little over the low level of early June. Pregnancy percentages increased substantially during July and reached

a second seasonal peak in August. The August lab data revealed that
the cost of reproduction was considerably lower than that of April
implying an expanded energy budget. Many females had apparently
recovered from the stress imposed by spring food shortages. However,
habitat availability underwent a decline in August resulting in the
exposure of most marginal vegetation. Although not nearly as severe as
May, a delayed response to the decline had detrimental consequences.
The September field sample revealed a slight decline in pregnancy
percentages suggesting limited mortality among reproducing females.
This drop occurred despite a dramatic increase in habitat availability.
Pregnancy percentages continued to decrease during the month of
September although habitat availability remained high. This was
probably primarily a function of a declining photoperiod.

Changes in reproductive patterns at the population level were the
result of size (age) specific responses to changes in food availability
mediated by changes in habitat availability. Small females were
generally nonreproductive and channelled energy toward somatic growth,
opting either for an improved physiological condition or greater future
fecundity afforded by a larger body size. In the early spring,
reproduction among small females lagged nearly a month behind that of
large females. Although a few large females continued to reproduce
through the reproductive slump in June and July, reproduction ceased
among small females until August. Many of these small females were
virgins or had only limited reproductive experience. A reduced food
supply has been shown to cause delayed maturation in rainbow trout
(Salma gairdneri) (Scott, 1962), brown trout (Salmo trutta) (Bagenal,

1969) and the three-spined stickleback (Gasterosteus aculeatus) (Wootton, 1973). However, small females had the capacity to respond rapidly to increased food availability. The minimum size of a reproducing female dropped 6 mm from August to September. This rapid response may have been in part a function of an improved physiological condition, since many of these females were virgins. Because large females remained reproductive throughout the season, much of the variation in pregnancy percentages and the mean size of reproducing females can be attributed to the patterns of reproduction among these small females.

From April to September, brood size did not change in response to fluctuations in food availability. The decreased brood size at the end of the reproductive season in October was probably the result of a declining photoperiod (Colson, 1969; Bowden, 1970). There is no reason to suspect monthly variation in the quality of eggs or young as only minor differences were revealed in samples obtained at extremes in food availability (April and August). Except for October, therefore, reproducing females were allocating the same quantity of energy to reproduction. Consequently, changes in food availability could be related directly to the cost of reproduction.

During periods of probable food limitations in spring, a female's total energy budget was reduced. The amount of energy allocated to reproduction was not correspondingly reduced, therefore, females were expending more effort in reproduction. The April lab sample indicated that much of the energy needed for reproduction was obtained from somatic tissue. This was especially true for large females. The

impact of this increased reproductive effort was decreased survivorship, particularly among large females. Smaller females had not incurred as great a cost and, consequently, had a higher survivorship. Moreover, in contrast to large females, smaller females curtailed reproduction during June and July in favor of increased growth and survivorship. Survivorship among small nonreproductive females was high, adding credence to the supposition that mortality was related to reproduction.

Increased food availability during the summer and, thus, an increased total energy budget, resulted in a decrease in reproductive effort. Consequently, the condition of reproducing, as well as non-reproducing females, improved significantly. The August lab sample indicated that females were not incurring as high a cost to reproduce as in April. However, large females still used somatic tissue to subsidize reproduction, possibly as a result of the decline in food availability in July. This resulted in some mortality among large females. This was evident by a slight decrease in both pregnancy percentages and the mean size of reproducing females. However, the decline in food availability and the associated mortality was not of the magnitude as that of spring.

The relationship between food, reproduction, and survivorship has been examined experimentally in surprisingly few studies, despite its important implications in the population dynamics of fishes. Wootton (1973, 1977) has demonstrated in laboratory studies on the three-spined stickleback, Gasterosteus aculeatus (Gasterosteiformes; Gasterosteidae) that food consumption during the interspawning interval

was not significantly correlated with egg production per spawning. Females were also found to tolerate a significant loss in body weight in order to subsidize egg production. However, starved females curtailed spawning in favor of survival. In laboratory studies on the Japanese madaka, Oryzias latipes (Oryziatidae; Cyprinodontiformes), Hirshfield (1980) found that increased food intake led to higher fecundity at two of three temperatures, while reproductive effort actually declined with food intake at two temperatures. The costs of reproduction included a reduction in the energy content of somatic tissue and substantial loss of mass in many fish that continued to reproduce at high levels. The number of moribund and dead females was significantly and positively correlated with reproductive effort and significantly and negatively correlated with changes in body mass.

The ovoviviparous reproductive biology of Poecilia latipinna and most other poeciliid species may be one solution to coping with habitats in which conditions can change very rapidly and, presumably, unpredictably. Females channel nutrients into eggs during a single yolk-loading period. All of the energy needed for the complete development of a full brood of embryos is prepackaged. Moreover, there is very little variation in the developmental stage of embryos in a brood, suggesting that eggs are loaded in a single wave. With no nutrient input to developing embryos, any energy assimilated by a pregnant female during the gestation period can be channelled toward maintenance (i.e. restoring somatic losses incurred during vitellogenesis) and growth.

This tactic has an associated cost. Periods of resource scarcity

may force females to not only rely more heavily upon somatic tissue to subsidize yolk-loading, but also result in considerable difficulty restoring somatic losses during the insuing gestation period. Female poeciliids apparently cannot recoup their reproductive investment through resorption of developing embryos (Meffe and Vrijenhoek, 1981). Consequently, a large commitment of somatic tissue during extended periods of resource limitations may be suicidal, resulting in the total loss of a reproductive investment.

The guppy, Poecilia reticulata, exhibits ovoviviparous reproductive biology similar to that of P. latipinna. However, there is more variation in developmental stage among embryos within a single brood, indicating that fertilization of all eggs does not occur simultaneously, but sequentially as they mature (Turner, 1937). Apparently, simultaneous production of a large brood of yolk-laden ova requires more energy than can be accumulated during the period available. Staggering egg development provides the foraging time needed to load all of the eggs (Thibault and Schultz, 1978). Hester (1964) reported that a reduction in food ration in P. reticulata decreased the number of oocytes capable of being fertilized and the number but not the size of young at birth. Mortality and brood abortion occurred among females on the lowest ration.

Other ovoviviparous species, such as Poeciliopsis monacha (Thibault and Schultz, 1978) and Poeciliopsis occidentalis (Constantz, 1979) circumvent the egg-loading/nutrient supply problem through superfetation. Instead of producing single large batches of eggs, energy is allocated in two separate periods. Thus, the surge imposed

by a single loading period is reduced (Thibault and Schultz, 1978).
When food is available, females allocate most of their energy to
reproduction. Under starvation stress, females curtail reproduction
in favor of survival; but a large number of secondary oocytes
accumulate (Meffe, 1979). Other ovoviviparous species that exhibit
superfetation may spread the cost of yolking eggs over as many as three
to five short intervals. Finally, truly viviparous species such as
Poeciliopsis prolifica and Poeciliopsis turneri produce eggs with very
little yolk but continuously supply nutrients to developing embryos.
During starvation stress, reproducing females of P. prolifica are
forced to subsidize developing embryos with somatic tissue. The cost
of this investment is a severe reduction in the survivorship of
reproducing females (Meffe, 1979).

Table 1. Summary of the results of the lab study for large and small females with young or eggs from samples taken in April and August. Values are means with standard deviations based upon 5 females of a given size and reproductive condition.

	April Sample				August Sample			
	Small Females		Large Females		Small Females		Large Females	
	Young	Eggs	Young	Eggs	Young	Eggs	Young	Eggs
Females								
SL(mm)	27.8 ± 1.04	27.6 ± 1.63	32.9 ± 1.94	35.2 ± 1.92	29.3 ± 0.17	27.6 ± 1.76	33.2 ± 1.10	33.8 ± 2.00
Adj. Wt. 1(mg)	110.70 ± 6.44	102.68 ± 6.44	224.02 ± 7.91	197.02 ± 7.91	157.63 ± 4.95	156.18 ± 4.95	251.30 ± 9.02	239.90 ± 9.02
Adj. Wt. 2(mg)	116.90 ± 8.84	97.79 ± 8.55	201.32 ± 6.27	209.18 ± 10.58	176.30 ± 8.84	145.61 ± 8.55	237.37 ± 6.27	268.71 ± 10.58
Cal./mg	5.38 ± 0.07	5.22 ± 0.07	5.28 ± 0.11	5.34 ± 0.11	5.90 ± 0.14	5.72 ± 0.25	5.64 ± 0.22	5.59 ± 0.24
% Lipid	12.92 ± 1.48	10.50 ± 1.50	10.78 ± 1.42	12.14 ± 0.58	19.24 ± 2.66	15.04 ± 5.93	17.64 ± 2.47	15.13 ± 5.23
Propagules								
Brood Size	8.6 ± 1.67	8.8 ± 1.92	15.4 ± 3.58	21.2 ± 2.49	8.2 ± 0.45	8.0 ± 1.30	13.4 ± 2.92	16.0 ± 5.66
Adj. Brood Size	9.1 ± 0.69	8.6 ± 0.78	15.6 ± 1.34	18.8 ± 1.34	7.7 ± 0.69	8.0 ± 0.78	13.2 ± 1.34	18.6 ± 1.34
Egg Dia.(mm)	---	2.50 ± 0.15	---	2.39 ± 0.19	---	2.35 ± 0.14	---	2.39 ± 0.17
Wt. (mg)	3.06 ± 0.58	4.02 ± 0.56	3.12 ± 0.53	3.69 ± 0.78	2.62 ± 0.38	3.62 ± 0.38	3.30 ± 0.73	3.62 ± 0.72
Cal./mg	5.69 ± 0.10	6.12 ± 0.09[1]	5.68 ± 0.09	6.29 ± 0.06	5.57 ± 0.24	6.19 ± 0.15	5.79 ± 0.07	6.30 ± 0.07
% Lipid	17.67 ± 0.56	15.19 ± 0.24[1]	17.29 ± 2.04	18.05 ± 0.97	15.46 ± 1.40	15.15 ± 1.65	18.08 ± 1.82	17.02 ± 1.56
Cal./Prop.	17.64 ± 2.98	24.32 ± 1.99	18.00 ± 2.52	22.82 ± 2.53	14.99 ± 1.86	22.84 ± 1.89	19.57 ± 4.10	22.75 ± 3.54
Lipid/Prop. (mg)	0.54 ± 0.12	0.60 ± 0.02	0.54 ± 0.08	0.70 ± 0.08	0.41 ± 0.07	0.55 ± 0.06	0.60 ± 0.11	0.62 ± 0.10

[1] based on only two clutches.

Table 2. Summary of statistical comparisons between females with term young and mature eggs in April and August samples. Original values are reported in Table 1. "+" indicates the larger of the two values being compared. * = marginally significant, $0.05 < \rho < 0.06$; ** $\rho < 0.05$; NS = not significant.

| | April Sample | | | | | | August Sample | | | | | |
| | Small Females | | | Large Females | | | Small Females | | | Large Females | | |
	Yng	Egg	Sign.	Yng	Egg	Sign.	Yng	Egg	Sign.	Yng	Egg	Sign.
SL (mm)	+		NS		+	NS	+		NS		+	NS
Adj. Wt. 1 (mg)	+		NS	+		*	+		NS	+		NS
Cal./mg	+		**		+	NS	+		NS	+		NS
% Lipid	+		**		+	NS	+		NS	+		NS

Table 3. Summary of statistical comparisons of April females and their broods to August females and their broods by reproductive condition and female size. Original values are reported in Table 1. "+" indicates the larger of the two values being compared. ** = $\rho < 0.05$; *** = $\rho < 0.01$; NS = not significant.

| | Term Young | | | | | | Mature Eggs | | | | | |
| | Small Females | | | Large Females | | | Small Females | | | Large Females | | |
	Apr	Aug	Sign.	Apr	Aug	Sign.	Apr	Aug	Sign.	Apr	Aug	Sign.
Females												
SL (mm)		+	NS		+	NS	identical		NS	+		NS
Adj. Wt. 2 (mg)		+	***		+	***		+	***		+	***
Cal./mg		+	***		+	***		+	***		+	**
% Lipid		+	***		+	***		+	NS		+	NS
Propagules												
Brood Size	+		NS	+		NS	+		NS	+		NS
Adj. Brood Size	+		NS	+		NS	+		NS	+		NS
Egg Dia. (mm)	---	---	---	---	---	---	+		NS	identical		NS
Wt. (mg)	+		NS		+	NS	+		NS	+		NS
Cal./mg	+		NS		+	NS		+	NS		+	NS
% Lipid	+		***		+	NS	+		NS	+		NS

Table 4. Summary of statistical comparisons between mature eggs and term young (propagules) by small and large females in April and August samples. Original values are reported in Table 1. "+" indicates the larger of the two values being compared. ** $\rho<0.05$; *** $\rho<0.01$; NS = not significant.

	April Sample						August Sample					
	Mature Eggs			Term Young			Mature Eggs			Term Young		
	Sml	Lrg	Sign.	Sml	Lrg	Sign.	Sml	Lrg	Sign.	Sml	Lrg	Sign.
Brood Size		+	**		+	**		+	**		+	**
Egg Dia. (mm)	+		NS	---	---	---		+	NS	---	---	---
Prop. Wt. (mg)	+		NS		+	NS	identical		NS		+	NS
Prop. Cal./mg		+	NS	+		NS		+	NS		+	NS
Prop. % Lipid		+	***	+		NS		+	NS		+	**
Cal./Prop.	+		NS		+	NS		+	NS		+	NS
Lipid/Prop. (mg)		+	NS	identical		NS		+	NS		+	**

Table 5. Summary of major differences between females with young and females with eggs by female size from April and August laboratory samples. Values labeled "Females" are based upon the mean dry weight of the 10 females within a given size group adjusted for differences in female SL (Adj. Wt. 1, Table 1). The mean cal/mg and % lipid in females of each size and reproductive condition (Table 1) were used in conjunction with Adj. Wt. 1 in calculating "Total Calorie Loss" and "Total Lipid Loss". Values labeled "Eggs" are based upon mean values that have not been adjusted for differences in female SL (Table 1). The values labeled "Relative Cost" are the ratio of "Total Calorie Loss" to "Total Brood Calories".

| Month | Size | Females | | | Eggs | | Relative Cost |
		Total Calorie Loss	Total Lipid Loss(mg)	SL Adj. Dry Wt. Loss(mg)	Unadj. Mean Brood Size	Total Brood Calories	% Brood Calories Subsidized by Body Calories
April							
	Small	59.58	3.52	8.02	8.8	216.50	28
	Large	130.74	0.23	27.00	21.2	492.05	27
August							
	Small	36.67	6.84	1.45	8.0	179.28	20
	Large	76.29	8.03	11.40	16.0	364.96	21
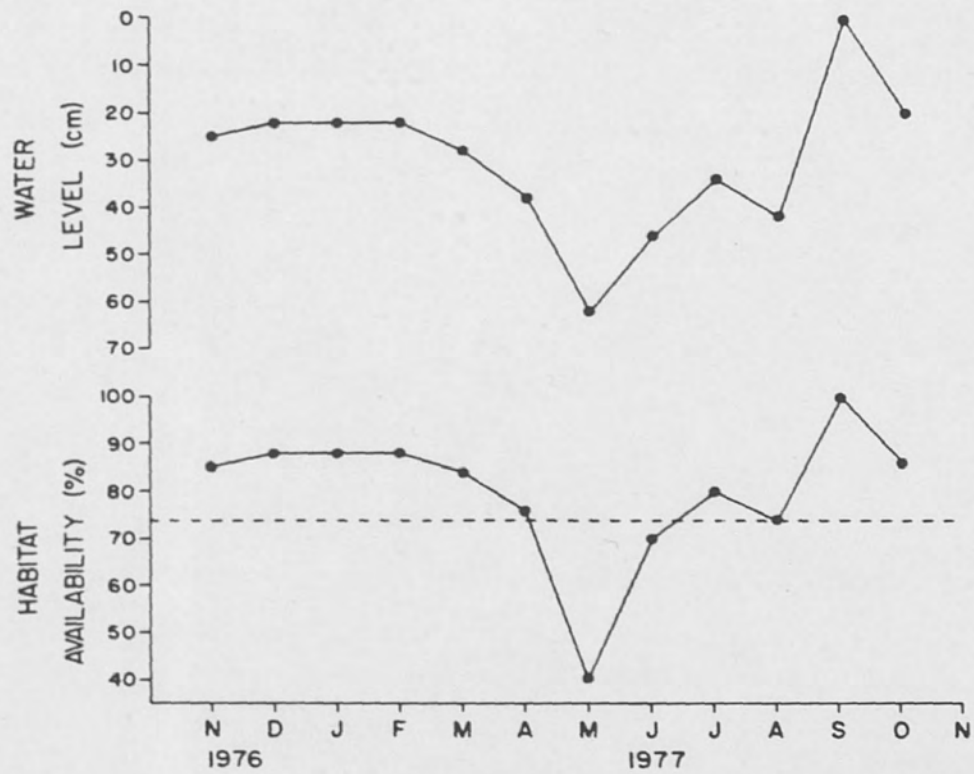
Figure 1. Changes in water level and habitat availability measured monthly from November 1976 to November 1977. See text for detailed explanation. At habitat availability of 75% or less, shallow marginal areas were exposed and unavailable.

FEMALE SIZE (mm SL)
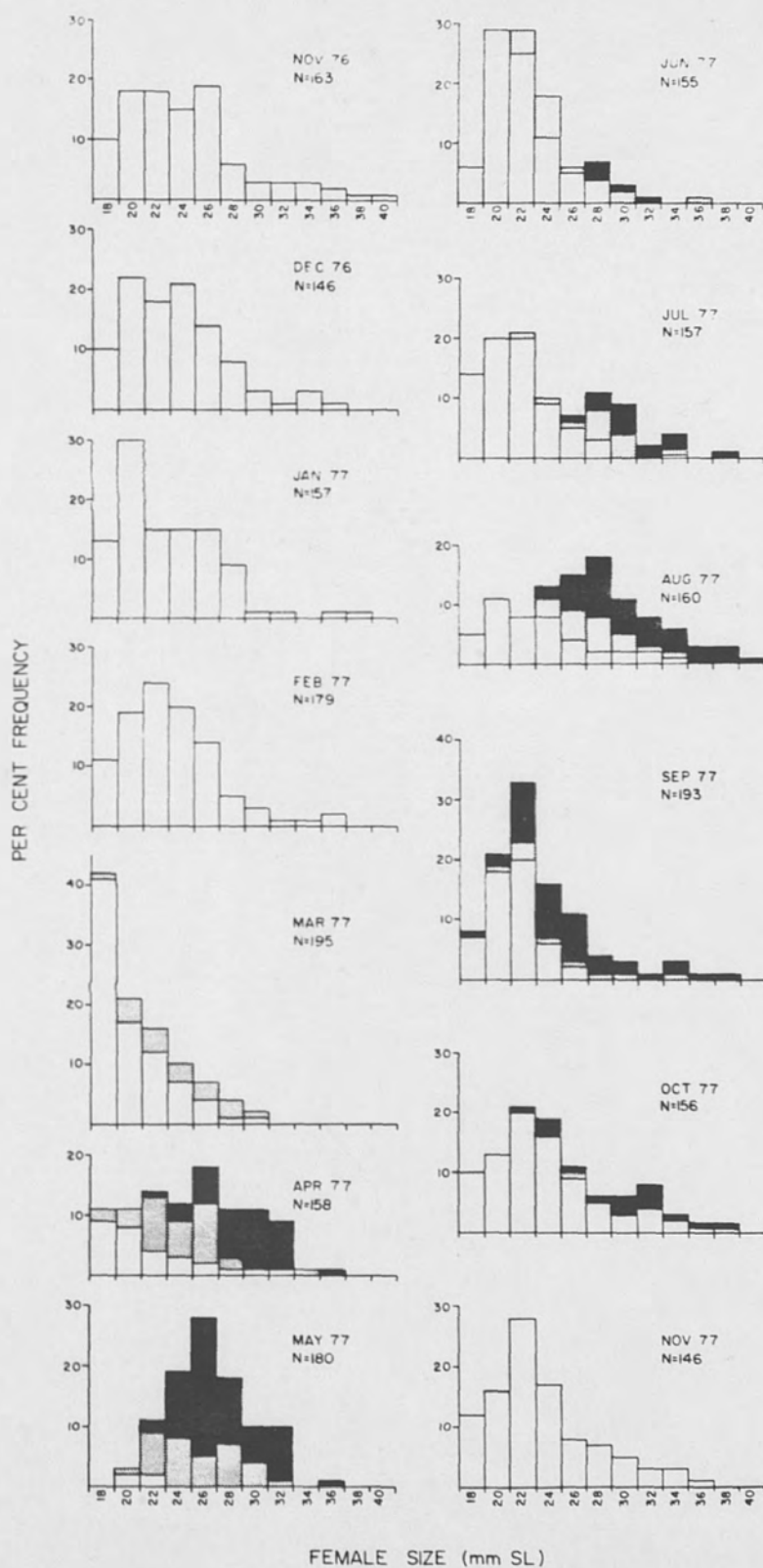
Figure 2. Monthly length frequency distributions of Poecilia latipinna by 2 mm size groups. Open bars, per cent females with undeveloped ovaries; stippled bars, per cent females with developing ova; black bars, per females with mature eggs or embryos.
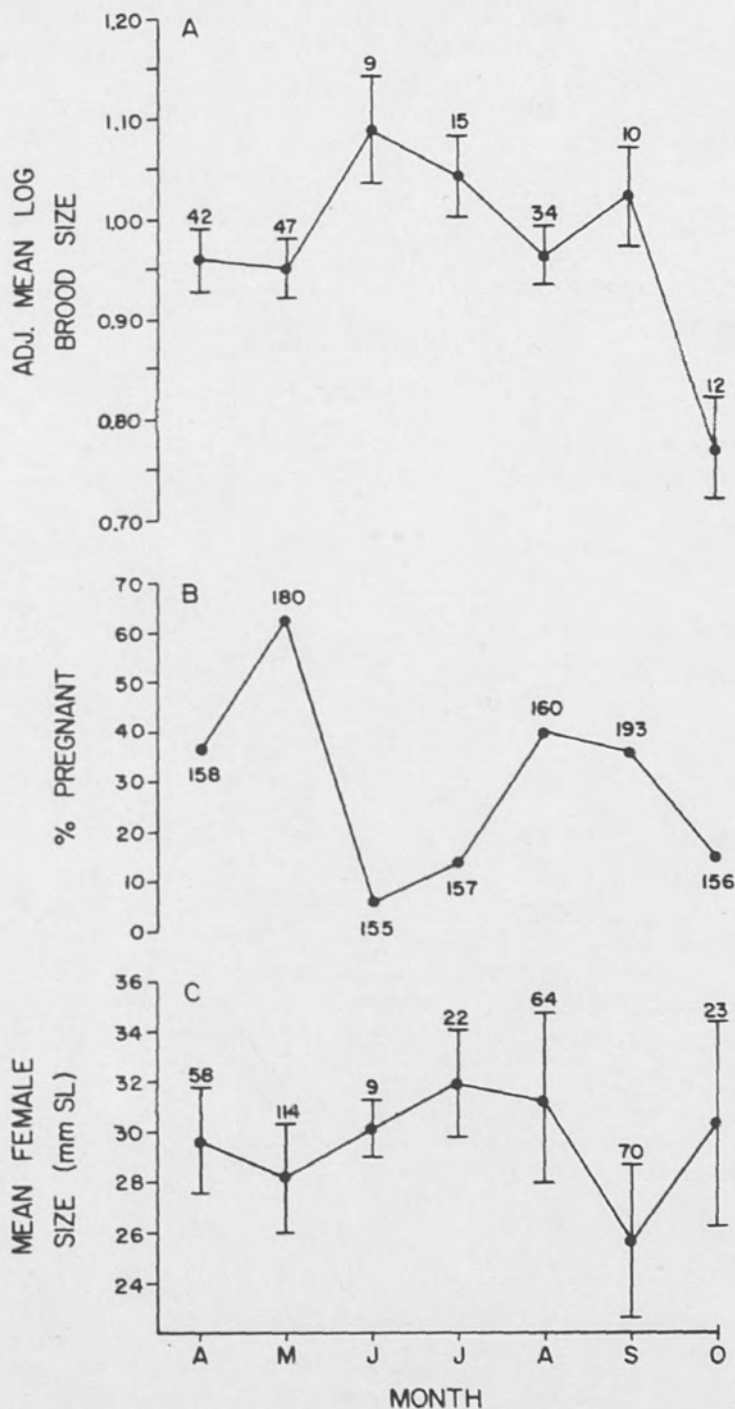
Figure 3. The monthly pattern of reproductive performance in
Poecilia latipinna. A. Adjusted mean ± one standard deviation of log
base 10 brood size. B. Per cent of females pregnant. C. Mean size ±
one standard deviation of pregnant females. Number at data points are
sample sizes.

Appendix Table I. Summary of the results of the lab study for large and small females with eggs from samples taken in April. Values are for individual females. Cal./mg and % lipid of females and eggs are means with standard deviations based upon 3 determinations. Dia. and wt. of eggs are means with standard deviations based upon brood size.

|	Small					Large				
	1002a[1]	1010a	1013a	1014a	1021a	1003b	1004b	1008b	1009b	1016b
Females										
SL (mm)	26.2	28.5	29.0	25.5	28.8	33.0	35.2	38.0	36.0	34.0
Wt. (mg)	87.03	114.26	109.60	83.78	114.04	159.96	226.01	258.57	259.18	200.69
Cal./mg	5.26 ± 0.13	5.32 ± 0.07	5.16 ± 0.05	5.17 ± 0.07	5.21 ± 0.10	5.47 ± 0.03	5.33 ± 0.08	5.18 ± 0.02	5.25 ± 0.05	5.33 ± 0.06
% Lipid	10.97 ± 0.86	8.34 ± 0.39	10.09 ± 0.18	10.80 ± 0.32	12.47 ± 0.43	12.70 ± 0.51	12.35 ± 0.53	11.87 ± 0.75	12.54 ± 0.49	11.26 ± 0.27
Eggs										
Brood Size	10	9	11	6	8	19	19	25	22	21
Dia. (mm)	2.40 ± 0.12	2.53 ± 0.12	2.63 ± 0.10	2.35 ± 0.07	2.51 ± 0.13	2.55 ± 0.19	2.42 ± 0.13	2.30 ± 0.08	2.33 ± 0.26	2.42 ± 0.12
Wt. (mg)	3.76 ± 0.48	4.14 ± 0.42	4.43 ± 0.60	3.49 ± 0.30	3.98 ± 0.49	3.59 ± 0.93	3.98 ± 0.32	3.18 ± 0.64	3.37 ± 0.71	4.32 ± 0.55
Cal./mg	6.04 ± 0.12	6.04 ± 0.08	6.24 ± 0.02	6.20 ± 0.06	6.10 ± 0.04	6.39 ± 0.06	6.26 ± 0.06	6.24 ± 0.03	6.29 ± 0.05	6.26 ± 0.05
% Lipid	15.36 ± 0.65	15.02 ± 0.74	---	---	---	19.62 ± 0.47	17.87 ± 0.26	17.27 ± 0.44	18.25 ± 0.27	17.29 ± 0.12

[1] female identification number

Appendix Table II. Summary of the results of the lab study for large and small females with young from samples taken in April. Values are for individual females. Cal./mg and % lipid of females and young are means with standard deviations based upon 3 determinations. Wt. of young are means with standard deviations based upon brood size.

	Small					Large				
	1017a[1]	1024a	1025a	1026a	1027a	1018b	1019b	1029b	1031b	1032b
Females										
SL (mm)	27.6	26.2	28.5	27.9	28.9	34.8	35.0	31.3	32.7	30.8
Wt. (mg)	118.75	106.65	120.16	79.29	132.49	249.75	246.42	157.10	176.67	164.48
Cal./mg	5.38 ± 0.06	5.46 ± 0.08	5.30 ± 0.07	5.34 ± 0.06	5.48 ± 0.08	5.34 ± 0.01	5.25 ± 0.03	5.44 ± 0.05	5.19 ± 0.01	5.17 ± 0.07
% Lipid	13.18 ± 0.50	14.73 ± 0.47	11.14 ± 0.55	---	12.73 ± 0.36	11.91 ± 0.64	9.65 ± 0.51	11.76 ± 0.64	8.93	11.85 ± 0.27
Young										
Brood Size	6	8	8	10	10	13	21	12	15	17
Wt. (mg)	3.39 ± 0.10	2.77 ± 0.11	3.79 ± 0.38	2.31 ± 0.16	3.25 ± 0.25	3.79 ± 0.41	2.94 ± 0.24	3.45 ± 0.49	2.58 ± 0.28	3.07 ± 0.36
Cal./mg	5.55 ± 0.08	5.72 ± 0.04	5.81 ± 0.07	5.70 ± 0.05	5.65 ± 0.12	5.74 ± 0.07	5.55 ± 0.09	5.77 ± 0.06	5.70 ± 0.07	5.64 ± 0.05
% Lipid	18.32 ± 0.47	16.88 ± 0.90	18.01 ± 0.46	17.73 ± 0.48	17.41 ± 0.22	15.69 ± 0.71	14.63 ± 0.70	18.33 ± 0.69	18.73 ± 0.33	19.25 ± 0.42

[1] female identification number

Appendix Table III. Summary of the results of the lab study for large and small females with eggs from samples taken in August. Values are for individual females. Per cent lipid of females and eggs are means with standard deviations based upon 2 determinations. Dia. and wt. of eggs are means with standard deviations based upon brood size.

| | Small | | | | | | Large | | | |
	1004a[1]	1007a	1013a	1019a	1026a	1003b	1009b	1010b	1027b	1028b
Females										
SL (mm)	26.9	27.0	26.3	27.1	30.7	37.1	32.1	32.4	34.1	33.4
Wt. (mg)	119.06	118.75	116.65	136.93	236.66	306.61	202.22	259.52	239.96	271.49
Cal./mg	5.73	5.63	5.36	5.82	6.05	5.31	5.69	5.56	5.45	5.93
% Lipid	14.23 ± 0.54	10.02 ± 0.15	14.36 ± 0.49	12.33 ± 0.03	25.39 ± 0.99	9.07 ± 0.20	16.57 ± 1.03	21.56 ± 1.15	10.51 ± 0.81	17.94 ± 1.15
Eggs										
Brood Size	7	10	8	9	7	22	12	10	22	14
Dia. (mm)	2.24 ± 0.11	2.34 ± 0.13	2.40 ± 0.07	2.37 ± 0.15	2.43 ± 0.16	2.32 ± 0.19	2.59 ± 0.06	2.40 ± 0.17	2.39 ± 0.16	2.39 ± 0.11
Wt. (mg)	3.26 ± 0.22	3.62 ± 0.45	3.84 ± 0.09	3.53 ± 0.36	3.88 ± 0.37	3.55 ± 0.73	4.61 ± 0.18	3.63 ± 0.59	3.41 ± 0.39	2.91 ± 0.53
Cal./mg	5.97	6.19	6.30	6.14	6.35	6.20	6.32	6.23	6.38	6.27
% Lipid	16.10 ± 0.80	12.62 ± 0.52	14.40 ± 1.07	16.44 ± 0.02	16.34 ± 0.91	14.59 ± 0.95	17.56 ± 0.81	16.52 ± 1.04	18.40 ± 0.91	18.18 ± 1.14

[1] female identification number

Appendix Table IV. Summary of the results of the lab study for large and small females with young from samples taken in August. Values are for individual females. Per cent lipid of females and young are means with standard deviations based upon 2 determinations. Wt. of young are means with standard deviations based upon brood size.

	Small					Large				
	1002a[1]	1008a	1024a	1032a	1033a	1020b	1021b	1023b	1030b	1030b
Females										
SL (mm)	29.3	29.5	29.5	29.3	29.1	34.7	32.5	33.9	32.1	32.6
Wt. (mg)	172.23	175.60	182.48	192.11	184.14	269.26	221.69	242.15	241.33	228.71
Cal./mg	5.74	5.87	5.83	5.93	6.11	5.42	5.43	5.93	5.76	5.65
% Lipid	15.82 ± 1.03	18.06 ± 0.98	20.01 ± 0.81	23.04 ± 0.32	19.56 ± 0.17	16.52 ± 0.11	14.57 ± 1.34	20.01 ± 0.54	20.41 ± 0.88	16.98 ± 1.22
Young										
Brood Size	8	9	8	8	8	18	12	13	11	11
Wt. (mg)	2.68 ± 0.07	2.46 ± 0.11	2.08 ± 0.39	2.97 ± 0.13	2.94 ± 0.16	2.75 ± 0.32	3.77 ± 0.38	2.76 ± 0.14	3.07 ± 0.21	4.53 ± 0.25
Cal./mg	5.75	5.78	5.50	5.62	5.19	5.69	5.82	5.76	5.87	5.83
% Lipid	16.16 ± 1.41	17.10 ± 0.03	12.32 ± 2.09	14.63 ± 0.93	14.03 ± 0.49	18.46 ± 0.11	20.41 ± 0.30	17.90 ± 1.09	18.46 ± 1.00	15.35 ± 0.67

[1]female identification number

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