Individual Variation and Competition in the Everglades Pygmy Sunfish

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INDIVIDUAL VARIATION AND COMPETITION IN THE EVERGLADES PYGMY SUNFISH

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SUMMARY

(1) Populations of Everglades pygmy sunfish (*Elassoma evergladei*, family Centrachidae) were manipulated in both the laboratory and the field to determine how individuals responded to changes in the intensity of competition.

(2) In laboratory experiments, individually identifiable fish were raised at different densities (sixteen, eight, four, and one fish per tank) and each individual's competitive ability was measured by its growth rate and reproductive condition. For females, estimates of reproductive potential were ovary weight and egg number. For males, reproductive ability was estimated by recording the frequency of occurrence of bobbing, a sexual behaviour. In field experiments fish were raised at the same densities but in screened enclosures to evaluate the realism of the laboratory experiments.

(3) Individual fish differed in their growth rates, and these differences were magnified under competitive conditions. Increased density also increased the variation among females within a population with respect to ovary size and egg number.

(4) Increased population density markedly decreased the growth rate of the 'average' fish in the population, but only slightly the growth of the 'best' competitors. In each density there were always some fish who grew as quickly as the 'average' fish of a population half as large.

(5) Increases in population size also produced non-linear reductions in estimates of both male and female potential reproductive success. For females these reductions could be attributed in part to density-induced reductions in growth rate. But density also had a direct effect on female reproductive success: for females of similar size or growing at a similar rate, those raised at higher densities had larger ovaries and more eggs.

INTRODUCTION

Competition has long been known as one of the major processes regulating the abundance and distribution of organisms. It is a process in which one organism attempts to divert resources from other organisms to itself for its own advantage and to the detriment of others. Yet despite numerous experimental studies and the elaboration of many mathematical models, the ways in which individuals affect, and are affected by, the competitive process remain poorly understood.

In part, this ignorance stems from the attempts of ecologists to explain competitive interactions by relying on simple mathematical models. These models, as outgrowths of the logistic model of single species population dynamics, assume (1) that all individuals in a population compete as equals and (2) that the competitive ability of the 'average' individual is unaffected by the density of the population. Ecologists realize that, as with

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most assumptions of ecological models, these conditions are rarely met, but they ignore the discrepancy because they presume the models to be robust and that differences will cancel each other out. As a result, few studies have measured the effects of competition on different individuals. The purpose of this study is to examine whether differences in competitive ability among individuals and the effects of population density on these abilities can be ignored without distorting our understanding of the process of competition.

MATERIALS AND METHODS

Experimental populations of individually identifiable pygmy sunfish were raised at different densities in the laboratory to examine (1) whether individual variation in growth rate, reproductive potential and survival resulted from competition for food and, if so, (2) whether the patterns of individual variation were affected by the size of the population. A field experiment in which fish were raised at the same densities, while the food levels varied naturally, tested the realism of the laboratory experiments.

The fish

The pygmy sunfish, *Elassoma evergladei* (Jordan), is a small benthic centrarchid about 3 cm long that lives in sluggish waters among the submerged vegetation. Carnivorous adults feed upon small annelids, chironomid larvae, daphnids, copepods and ostracods (Barney & Anson 1920; D. I. Rubenstein unpublished). They mature at about one year and rarely live more than three years (Barney & Anson 1920). In North Carolina the breeding season begins in late March and continues through July. A female is capable of laying as many as 300 eggs (Barney & Anson 1920). Although reports are contradictory, it appears that *Elassoma*, unlike most centrarchids, do not make nests (Bertholdt 1953; Mayer 1955); the shed eggs simply adhere to the submerged vegetation. Larval growth is rapid and for individuals hatched early in the season, adult size is reached by the time water temperatures drop in late November.

The pygmy sunfish was chosen for this study because:

(1) It is carnivorous and eats only living prey. Its diet could therefore be accurately controlled and manipulated.

(2) It is small and could be kept in 38-litre aquaria without markedly distorting its behaviour (but see Martin 1975 for evaluation of the problem of confinement on behaviour). In addition, many replicate populations could be maintained, thus permitting powerful statistical analyses.

(3) It is hardy and showed no apparent ill-effects associated with transport or experimental handling.

(4) It is primarily a solitary fish. The fact that it does not shoal and is occasionally territorial under certain conditions of prey dispersion (Rubenstein 1981), makes it ideally suited for a study of competition because beneficial effects of neighbours, so often upset in laboratory systems, are of minimal importance anyway.

(5) It normally lives in small ponds that undergo radical seasonal changes in volume, and therefore under natural conditions the pygmy sunfish experiences wide fluctuations in population density.

Laboratory experiments

Young fish were raised at different densities under semi-natural conditions. The experiments lasted from the early October, to the onset of the breeding season in April.

Small sub-adult fish were collected in mid-September from the Green Swamp in Brunswick County, North Carolina, and placed in separate containers for 2 weeks. This period of isolation served to minimize differences in past experience and to allow identification of fish damaged by handling. Each fish was weighed and photographed for length determinations. The unique spot pattern of each individual was recorded on fish silhouettes to avoid the need to mark individuals artificially. Fish were weighed by blotting them on a cloth towel and then immersing them in pre-weighed beakers of water. The lengths of fish were measured from photographs of individuals in a shallow pan of water containing a millimeter scale.

A total of fifteen experimental populations were established: three populations of sixteen fish, three of eight fish, three of four fish, and six of only a single fish. Since pygmy sunfish are solitary, or even territorial, fish raised in isolation served as competition-free controls. Fish were divided into three weight classes. From each weight class, fish were chosen at random and assigned to one replicate population of each density. Because *Elassoma* are sexually monomorphic at this time of year (see Rubenstein 1981), it was not possible to assign equal numbers of males and females to the populations.

Each population, regardless of density, was placed in an aquarium (38-litre) containing 3 cm of autoclaved stream sand, four small red clay flower pots, and four living plants. Seasonal patterns of day length and water temperature were maintained throughout the experiment.

The laboratory experiments were designed so that the fish at the higher densities would compete more vigorously for food. Therefore, each aquarium, regardless of fish density, was supplied with an identical amount of food, twenty prey items every other day. The diet consisted of mixtures of chironomid larvae (*Chironomus* sp.) and small annelids (*Tubifex* sp.) which were collected from nearby streams. Prey items were haphazardly dropped in small clumps about the bottom of the aquaria. In the experimental tanks all the food was eaten within 1–20 min, depending on the density of the population. Only in the control tanks did food occasionally remain uneaten for several hours after presentation. In the few instances (7) where prey remained uneaten after 6 h, the excess was removed. To maximize the likelihood that competition for food was responsible for the competitive outcome and not the effects of growth inhibitors (Yu & Pearlmutter 1970; Solomon (1977), the water of each aquarium was filtered.

Preliminary studies showed that weight, rather than length, was the more important variable determining body size. Consequently, in order to determine growth trajectories, each fish was weighed at approximately 30-day intervals. Growth rates of individual fish were estimated by fitting a linear regression of body weight on time.

Potential male reproductive success was estimated at the onset of the breeding season by measuring the frequency of occurrence of bobbing, a distinct sexual display. Bobbing behaviour appears at the beginning of the breeding season and is used only in courtship. It was assumed that the frequency of this behaviour indicated the likelihood of successful breeding. Males were observed for 10-min periods after the cessation of feeding for about 2 weeks, just prior to the termination of the experiment. The males were autopsied at the termination of the experiment, and all but the smallest male in one high density population were producing sperm.

Potential female reproductive success was estimated by measuring ovary net weight and egg number. The experiment was terminated when a majority of females had extended abdomens and were ready to lay eggs. At this time, females were weighed and then anaesthetized in MS 222 (tricane methane sulfonate). The ovaries were removed and

after 3 min of air drying were weighed on an electronic Cahn balance reading to 0·01 mg. The eggs were then dispersed in a small amount of water and counted.

Field experiments

The field experiments were designed to evaluate the realism of the results obtained from the laboratory experiments. Fifteen wooden frames covered with fibreglass screen (60 × 30 × 30 cm; 7 meshes/cm) were placed in the pond from which the fish used in the laboratory experiments were collected. Juvenile fish, just large enough not to pass through the screen, were collected and weighed to 1 mg precision. As in the laboratory experiments, fish similar in weight were divided into density groups. Three populations containing sixteen, eight and four fish, and six populations containing only a single fish were assigned at random to cages.

The cages were partially submerged at one end of the pond and provisioned with a small amount of sun-dried debris from the pond bottom. No additional food was added because benthic animals and pelagic microcrustaceans could enter the cages. Thus, unlike the conditions of the laboratory experiment, food levels were allowed to fluctuate.

The field experiments were established in July 1975. In March 1976, at the start of the breeding season, the surviving fish were removed and weighed. As before, the females were anaesthetized in MS 222, and their ovaries were removed and weighed.

Because these fish were too small to be individually identified at the start of the experiment, distributions of body size and female fecundity at the termination of the experiment were used to determine how individuals were affected by density under more natural conditions.

RESULTS

Laboratory experiments

Growth rate

Inspection of the growth trajectories for the six fish grown alone (Fig. 1(a)) shows that even under conditions of no competition there was variation in growth. An analysis of covariance showed that the estimates of these growth rates were significantly different ($F_{5,30} = 52·45$, $P < 0·0001$). Thus, there appear to be genetic factors or chance environmental events that influence an animal's ability to grow. Even though these factors had a significant impact on growth rate, the relative position of a fish at the beginning of the experiment, in terms of body size, was generally maintained throughout the experiment.

Representative growth trajectories of fish raised at higher densities also show patterns of variation (Fig. 1(b)–(d)). Clearly, the degree of inequality increased as population density increased. At the lowest competitive density (four fish/tank, Fig. 1(b)), the overall pattern of growth was very similar to that of the controls, except that the variation among individual growth trajectories was somewhat greater under the competitive conditions. At the intermediate density treatments (eight fish/tank, Fig. 1(c)), the pattern

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FIG. 1. Representative growth trajectories of the fish raised at different densities under semi-natural conditions. Solid lines denote males and dashed lines denote females. Stars depict sexually displaying males. A trajectory terminating before the end of the experiment depicts the death of the fish. (a) Six fish raised alone, (b) four raised together, (c) eight fish raised together, (d) sixteen fish raised together.
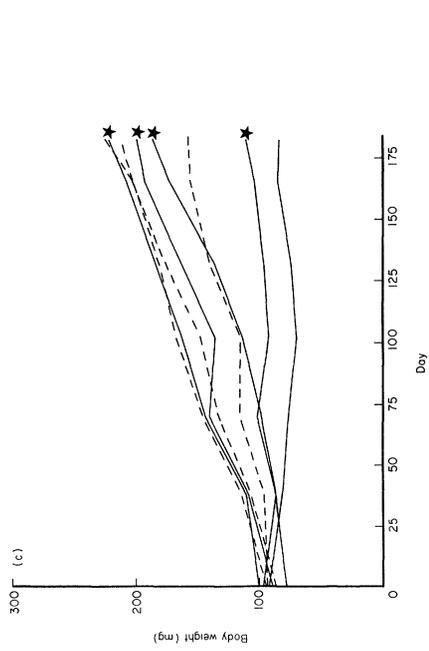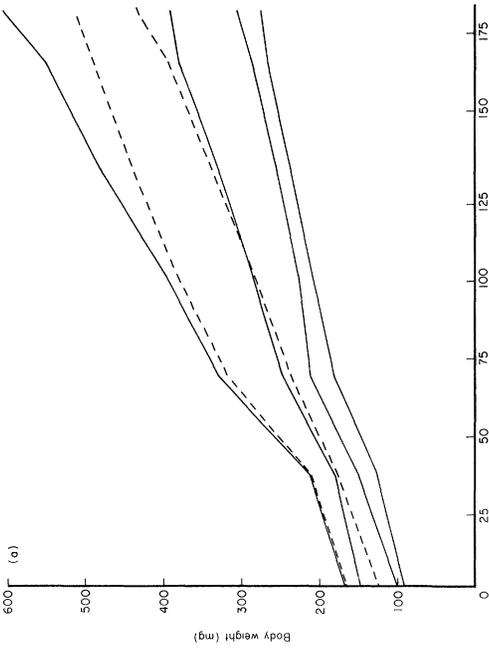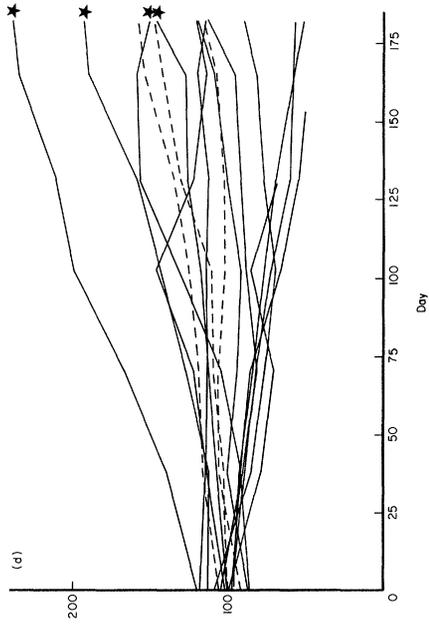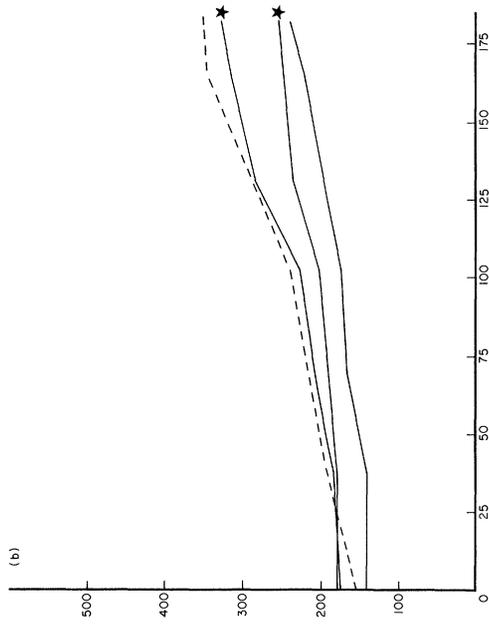
TABLE 1. Mean, mean-maximum, and total growth rates for densities of sixteen,
eight, four, and one fish per tank

Density	Replicate	Mean growth rate (mg/day)	Mean-maximum growth rate (mg/day)	Total growth rate (mg/day)
1	1	1·63	2·27	1·42
	2			2·02
	3			2·51
	4			1·71
	5			1·09
	6			1·04
4	1	0·77	1·02	3·07
	2	0·94	1·31	3·76
	3	1·05	1·39	4·21
8	1	0·42	0·64	3·40
	2	0·49	0·83	3·90
	3	0·47	0·72	3·82
16	1	0·12	0·46	1·75
	2	0·10	0·59	1·65
	3	0·11	0·47	1·81

deviated markedly from that of the control; no longer did all fish exhibit a net weight gain over the experimental period. At the highest competitive density (sixteen fish/tank, Fig. 1(d)), the majority of the fish showed only marginal increases in body weight, while some actually lost weight over the experimental period. The effects of competition were so severe in the high density populations that a number of fish died, apparently of starvation. The instantaneous growth rate of each fish was estimated by the slope of the regression of body weight on time. When the amount of growth variation, or competitive inequality, exhibited by each population is summarized by the coefficient of variation of the slopes ($CV_1 = 34 \cdot 9$, $CV_4 = 45 \cdot 2$, $CV_8 = 51 \cdot 9$, $CV_{16} = 208 \cdot 5$), the differences among densities are significant ($F_{2,6} = 26 \cdot 4$, $P < 0 \cdot 005$).

Increasing density decreased not only the mean growth rate of all the fish (the 'average' fish), but also that of the two fastest growing fish (the 'best' competitors) in each replicate, but in different ways. Table 1 shows that the growth of the best competitors did not decrease nearly as fast as that of the average fish, especially at the highest density. In fact, the two best competitors in the high density populations grew on average as well as the average fish in the intermediate density populations. Thus, despite the increased intensity of competition in the highest density population, the best competitors grew as if only slightly affected by the presence of additional conspecifics.

Table 1 also shows that the summation of the growth rates within a population (total growth rate) vary in a non-linear fashion with increasing density. The total growth rate of the low and intermediate density populations was approximately equal and was significantly higher than that of the control and high density populations. Since all treatments lasted for the same length of time, these differences reveal that moderate levels of competition result in the most efficient conversion of prey into fish biomass. This suggests that conversion efficiency declines under conditions accentuating competitive inequality

Female reproductive potential

The effects of density on female reproductive potential were dramatic. First, populations raised at different densities differed with respect to average female ovary weight and egg number (Table 2). At the higher densities where competition was more severe, females

TABLE 2. Means and coefficients of variation of ovary weight and egg number for females raised at different densities

Density	Number of females	Ovary weight		Egg number	
		Mean	C.V.	Mean	C.V.
1	2	23·4	–	500·0	–
4	3	13·6	44·4	280·3	28·6
8	8	5·6	54·6	139·1	59·8
16	11	3·5	75·7	115·0	83·8

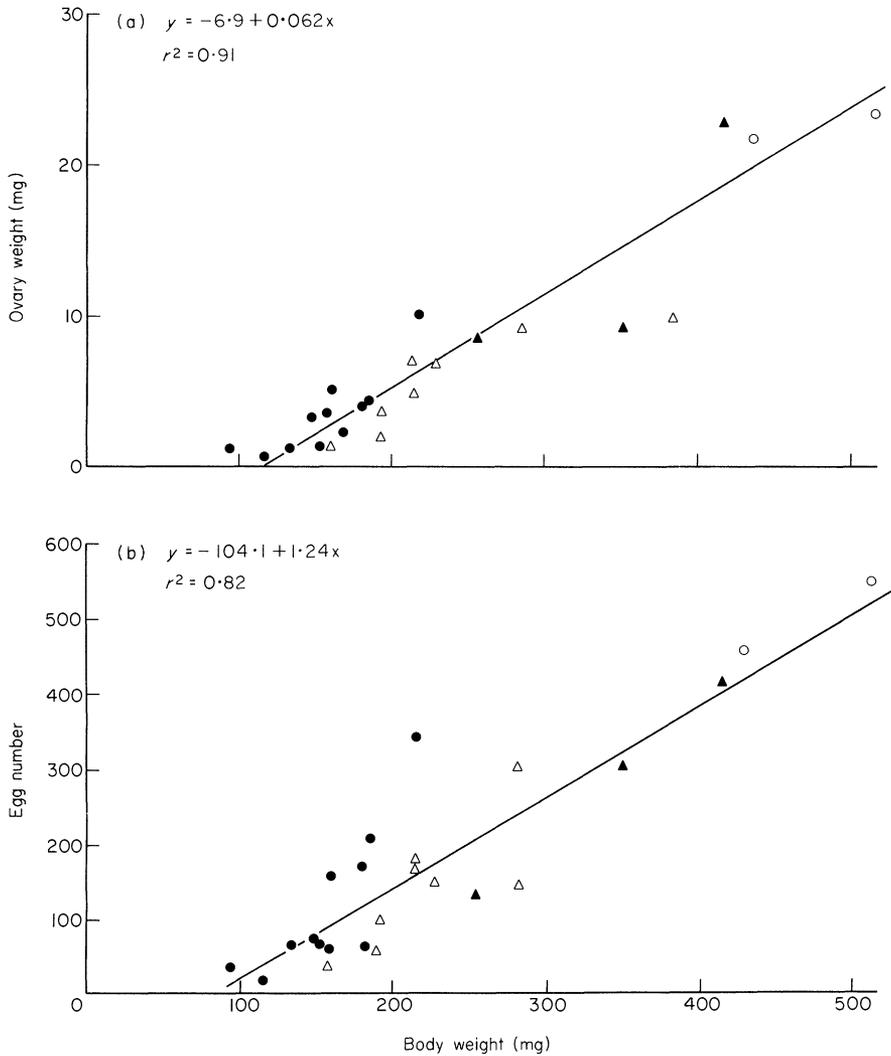FIG. 2. Relationship between (a) female body weight and ovary weight and (b) of female body weight and egg number. ● denotes females from high density populations; △ denotes females from intermediate density populations; ▲ denotes females from low density populations; and ○ denotes females raised alone. The correlation between ovary weight and egg number was highly significant ($r = 0.93$, d.f. = 22, $P < 0.01$).

had significantly smaller ovaries and fewer eggs. Second, the variation among female reproductive potential was affected by population density (Table 2). As density increased, both the coefficients of variation of ovary weight and egg number increased. Thus, as with growth rate, some females at the higher densities were behaving as if hardly affected by the presence of large numbers of competitors. That some females from the higher density treatments had ovaries as large as, or containing as many eggs as some of the females raised at lower densities, emphasizes the magnitude of density-induced intra-populational differences.

While it is clear that on average female reproductive potential varied inversely with density, it is still important to determine whether the effects of competition on fecundity were indirectly mediated through body size or growth rate differences, or whether there were additional direct effects of density on fecundity. Support for the indirect role of density is shown in Fig. 2 by highly significant relationships between a female's body weight and the weight of her ovary ($r = 0.95$, d.f. $= 22$, $P < 0.001$) and between a female's body weight and the number of eggs she was carrying ($r = 0.89$, d.f. $= 22$, $P < 0.001$). These relationships were caused by the experimental competitive treatments, because there was no significant correlation between a female's ovary weight at the end of the experiment and her body weight at the start of the experiment ($r = 0.31$, d.f. $= 22$, $P > 0.05$). A similar analysis performed on both fecundity measures and growth rate yielded the same results. An analysis of covariance was used to determine whether all females of a given size or displaying equivalent growth rates were investing the same proportion of their reserves in current reproduction regardless of population density; or whether those experiencing more intense competition were disproportionately investing resources in, or withholding resources from, current reproduction. The regressions of body weight, or growth rate, on ovary weight did not differ significantly among densities (Table 3). Therefore, the ovary weights of females raised at different densities were compared after adjusting for body size or growth rate differences (Table 3). The fact that these adjusted ovary weights were significantly different and varied inversely with density (Table 3), showed that there were direct effects of density on fecundity in addition to those indirectly mediated through changes in growth rate. For any given body size, or growth rate, females suffering higher levels of competition have significantly larger ovaries and more eggs than did females experiencing lower levels of competition.

It is interesting to note that in spite of density-induced adjustments by females in the proportion of resources devoted to current reproduction, the average material investment

TABLE 3. Analyses of covariance of ovary weight and egg number on density and body weight or growth rate

	Residual d.f.	Body weight Residual MS	F	p	Residual d.f.	Growth rate Residual MS	F	p
Ovary weight								
Common slope	20	3·920	19·00	<0·001	20	4·384	167·8	<0·001
Equality of slopes	16	2·803	1·40	NS	16	2·659	1·16	NS
Equality of intercepts	18	2·927	4·59	<0·05	18	2·706	7·33	<0·01
Egg number								
Common slope	20	3999·0	17·02	<0·001	20	4735·0	16·29	<0·001
Equality of slope	16	2946·0	1·28	NS	16	3781·0	0·31	NS
Equality of intercepts	18	3038·0	4·29	<0·05	18	3492·0	4·21	<0·05

per egg appeared not to vary significantly ($t_{17} = 1\cdot58$; $P < 0\cdot20$). The average size of the eggs of females raised at low and intermediate densities were nearly identical ($\bar{X}_{\text{low}} = 0\cdot042$ mg/egg; $\bar{X}_{\text{Int.}} = 0\cdot043$ mg/egg), whereas those of females raised at the high density were slightly smaller ($\bar{X}_{\text{high}} = 0\cdot034$ mg/egg).

Male reproductive potential

There was much variability among males in the frequency with which they displayed the sexual bobbing display. Because the experiments were terminated before any matings occurred, it was difficult to estimate reliably male reproductive potential. A male was considered to be sufficiently active and capable of mating if during the observation periods it displayed at least once on four of the eight feeding days prior to the termination of the experiment.

Table 4 shows the proportion of males actively displaying at different densities. The differences between densities were significant ($F_{2,5} = 17\cdot67$, $P < 0\cdot01$). As density increased, the proportion of males sexually displaying decreased but, according to the Duncan multiple range procedure, only in the highest density populations were the number of displaying males significantly reduced. The stars in Figs 1(b)–1(d) depict the growth trajectories of males meeting the above criteria for sexual activity. In all cases, these were the fastest growing males in the population. Thus, even though density reduced the proportion of males actively displaying towards females, the best competitors in each population became sexually active and increased their chances of mating.

Field experiments

Because of a severe drought, only two replicate populations at each density were submerged at the termination of the experiment. As shown in Table 5, there were significant differences in the percentage survival among the density treatments ($F_{2,3} =$

TABLE 4. Number and proportion of males estimated to be reproductively active in each density population

Density	Replicate	Number of males in population	Number of active males	Proportion of active males
16	1	10	3	0·30
	2	13	4	0·31
	3	13	3	0·23
8	1	6	4	0·67
	2	5	4	0·80
	3	5	4	0·80
4	1	3	2	0·67
	2	4	–	–
	3	2	2	1·00

TABLE 5. Summary of field experiment data

Initial density	Final density	Survival (%)	Mean initial weight	Mean final weight
4	4	100	42·25	179·75
4	4	100	57·25	127·00
8	6	75	46·25	157·00
8	7	88	60·50	144·71
16	7	44	49·44	104·43
16	9	56	56·38	103·11

24·50, $P < 0.025$). The change in percent survival, however, appears to be non-linear. As density was doubled from four to eight fish per cage, the percentage survival was reduced by 18% but as density was doubled from eight to sixteen fish per cage, the percentage survival was reduced by 39%.

The relationship between initial and final body weight distributions was also affected by population density. Table 5 shows the means of the initial and final weights of the fish placed in those cages that remained submerged throughout the experiment. Although the initial weights differed significantly between replicates within each density ($F_{3,50} = 13.86$, $P < 0.001$), the initial weights were not found to differ significantly among densities ($F_{2,50} = 0.98$, $P > 0.05$). At the termination of the experiment, there were no longer significant differences in body weight between replicates, but there were significant differences among densities ($F_{2,31} = 7.68$, $P < 0.002$). The Duncan multiple range procedure showed that the sizes of the average fish grown at low or intermediate densities were not significantly different, but that the sizes of the average fish raised at the highest density were significantly lower than those raised under more moderate conditions.

That the high and intermediate density treatments showed significant differences in mean body size, even though the final densities of the two treatments were very similar, suggests that there were strong historical components of competition. Animals that eventually died in the course of the experiment still garnered resources while alive and thus, by initially reducing the growth rates of the ultimate survivors, affected their final body weights. In fact, the symmetrical shape of the distribution of final body weights at the highest density may be the result of the poorest and smallest competitors dying prior to the end of the experiment.

Female reproductive potential was also affected by density. Because only two females survived in the low density populations, only the high and intermediate density populations were used to determine the effect of density on female fecundity. Density had a dramatic impact on the reproductive condition of females. At the highest density, four of the nine females had no mature eggs, whereas at the intermediate density only one of five females
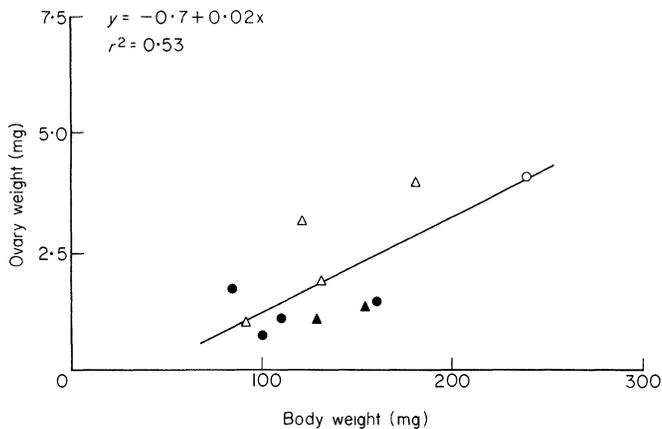

FIG. 3. Relationship between female body weight and ovary weight of those females in the field experiment having mature eggs. ● denotes females from high density populations; △ denotes females from intermediate density populations; ▲ denotes females from low density populations; and ○ denotes females raised alone.

lacked mature eggs. Density also affected ovary weight among females with mature eggs. Females raised in high density populations had significantly smaller ovaries than females raised in intermediate density populations ($F_{1,12} = 5·65$, $P < 0·05$). As in the laboratory experiments, there was a significant regression of ovary weight on body size (Fig. 3), and this relationship was not significantly different for the two densities ($F_{1,10} = 3·89$, $P = 0·08$). An analysis of covariance performed on ovary weights adjusted for differences in body size showed no significant differences among the high and intermediate density populations ($F_{1,11} = 3·15$, $P = 0·10$). Thus, in the field there were no direct and disproportionate effects of density on fecundity. Density affected female fecundity only by influencing growth rate and hence body size. It may have been the case that the increased death rate in the high density populations reduced the intensity of competition sufficiently so as to eliminate any direct density effects. It should be noted, however, that because of small sample sizes the null hypothesis was easily accepted.

In summary, the field experiments demonstrated individual differences in body size and fecundity which were the result of density. In general, the laboratory experiment, except for inflated survival values, did not significantly distort the natural pattern of density-dependent effects. The lowered survival rates in the field experiments were probably caused by small insect predators, such as odonate larvae, entering the cages and eating the smaller, weaker fish.

DISCUSSION

These experiments were designed to examine the biological realism of some of the assumptions underlying simple models of population dynamics, such as the logistic model, and to determine whether ignoring the implications of these assumptions limits our understanding of competition.

The results clearly show the assumption of equal competitive abilities to be false. There was inherent variability among individuals in their ability to grow and produce eggs, but competition magnified these differences. The results also show that the depressing effects of conspecifics on the 'average' individual's contribution to the growth of the population (*per capita* contribution estimated by expected fecundity) were not in proportion to the reciprocal of population size as predicted by the logistic equation, largely because increases in density induced females to shift resources from growth to current reproduction. In effect, female pygmy sunfish raised under stressful conditions were behaving as if they were minimizing the short-run effects of intensified competition. (According to life history theory, this is to be expected if adult survival prospects are low [Schaffer & Gadgil 1975].) But unlike brown and rainbow trout which also show a competitively induced shift in reproductive effort (Bagenal 1969; Scott 1962), the pygmy sunfish's increased reproductive effort does not result in the production of larger eggs, just more of them. This suggests that factors affecting the survival prospects of the young in the wild, such as predation or the abundance of larval food, may affect allocation strategy.

More importantly, the results show that ignoring individual differences in ability between animals does in fact distort our understanding of competition. Increasing density decreases mean growth rate and mean fecundity, but focusing on averages obscures the fact that the growth rates and expected reproductive outputs of some individuals in each population are greater than, or equivalent to, those of the 'average' individual in populations half as large. And, as the results of the field experiment demonstrate, one consequence of

competitively accentuated differences among individuals is that some fish grow so slowly that they die from predation or other mortality factors before attaining an adequate size for reproduction. Determining how such ongoing adjustments in population size and in an individual's reproductive potential affect the dynamics of the population, will depend on whether the effects are felt equally by members of both sexes, and whether the population is monogamous or polygamous. Regardless of which situations pertain, accounting for variations in individual ability will affect population processes. Theoretical studies have already demonstrated this for patterns of metamorphosis (Wilbur & Collins 1973), and optimal group sizes (Rubenstein 1978) as well as the dynamics and stability of populations (Łomnicki 1978). And since competitively induced variation in individual growth and survival has been found in green sunfish (Allee *et al.* 1948), rainbow trout (Li & Brockson 1977), medaka (Magnuson 1962), gobies (Yamaghishi, Maruyama & Mashiko 1974), platyfish (Sohn 1977), blowfly larvae (Nicholson 1954), and a variety of species of amphibian larvae (Rose 1960; Wilbur 1976, 1977; Steinwascher 1978), the effect should be widespread.

Focusing on individuals may also provide important insights into the structure of biological communities, particularly in guilds (Root 1967) where variations in individual abilities irrespective of species might be more important in determining inter-specific competitive relationships than are average taxonomic differences (Wilbur 1976), or in the tropics where population densities per species are low but the number of species is high (J. Travis, pers. comm.). In predator-prey situations, differential predation on animals differing in competitive ability might have dramatic effects on the dynamics of the population and on its place in the community. If a predator concentrated its attack on the largest, fastest growing, and most highly fecund members of a population, the ecological implications might be very different than if the predator concentrated its attack on the smaller, weaker, and less fecund members of a population. If predation eliminated the best competitors, those most efficient at converting energy into offspring, then the newly-released resources might not be efficiently used by the remaining individuals who are the poorer competitors. If they produce fewer offspring than the better competitors would have produced, or if some of the resources are lost to other species, then the whole structure of the community would be altered. If the predator concentrated its attack on the weaker members of the population, then the liberated resources would most likely be consumed by the remaining top competitors of the species, and the structure of the community would thus be preserved.

Accounting for variation among individuals in competitive ability may also have potential economic value for the fishing industry. For many species of fish, limits have been placed on the minimum size of fish that can be harvested. These refuges allow immature fish to grow and replenish the fishery. But, placing an additional upper limit on the size of fish that could be harvested should expand the fishery at an even faster rate. The largest fish, those generally demonstrating the best competitive abilities, would then continue to grow and reproduce. The reproductive output of this size class would have a dramatic effect on increasing the size of the fishery.

The results of this study demonstrate that ecologists should focus on individuals. This can be accomplished in part by describing populations not only in terms of size and average responses, but in terms of variance and skewness as well. Distributions of competitive outcomes, however, only provide limited information about the process of competition because they ignore the means by which animals compete and the 'inter-mediate' outcomes that feed back on the mechanisms and are instrumental in determining

the 'ultimate' outcomes, such as body size, reproductive potential and survivorship. I show elsewhere that the relationship between mechanisms and proximate and ultimate outcomes in pygmy sunfish is complex (Rubenstein 1981). The tactics by which male pygmy sunfish compete for food vary depending on the number of competitors and the dispersion of prey. At all densities when prey repeatedly appeared in a centrally situated clump, all males established territories, and variation in individual growth rates was accentuated. In the highest density population, however, these differences among individuals were significantly reduced because males adopted different territorial competitive strategies, depending on their size. Whereas the larger males defended territories adjacent to the spot where the clump regularly appeared, the smaller subordinate males defended peripheral territories. By occasionally seizing food as sneaky raiders, they acquired significantly less food than the centrally located dominants, but by engaging in significantly fewer aggressive encounters they reduced their energy needs. As a result of these two different patterns of behaviour, the growth differences among individuals were minimized. It is likely that for many species in which dominance relationships, territorial exclusion, and non-random mating occur, complex interactions between mechanisms and outcomes will exist. If ecologists are to evaluate the consequences of individual variation on the dynamics of populations and communities fully, such interactions must be deciphered and incorporated into ecological theory.

ACKNOWLEDGMENTS

REFERENCES

Allee, W. C., Greenberg, B., Rosenthal, G. M. & Frank, P. (1948). Some effects of social organization on growth in the green sunfish, *Lepomis cyanellus*. *Journal of Experimental Zoology*, **108**, 1–19.

Bagenal, T. B. (1969). The relationship between food supply and fecundity in brown trout *Salmo trutta* L. *Journal of Fish Biology*, **1**, 167–182.

Barney, R. C. & Anson, B. J. (1920). Life history and ecology of the pygmy sunfish *Elassoma zonatum*. *Ecology*, **1**, 241–256.

Bertholdt, W. (1953). Breeding *Elassoma everglaidei*. *Aquarium Journal*, **24**, 87–89.

Li, H. W. & Brockson, R. W. (1977). Approaches to the analysis of energetic costs of intraspecific competition for space by rainbow trout (*Salmo gairdneri*). *Journal of Fish Biology*, **11**, 329–341.

Lomnicki, A. (1978). Individual differences between animals and the natural regulation of their numbers. *Journal of Animal Ecology*, **47**, 461–475.

Magnuson, J. J. (1962). An analysis of aggressive behavior, growth, and competition for food and space in medaka (*Oryzias latipes*) (Pisces, Cyprinodontidae). *Canadian Journal of Zoology*, **40**, 313–363.

Martin, R. G. (1975). Sexual and aggressive behaviour, density and social structure in a natural population of mosquito fish, *Gambusia affinis* holbrooki. *Copeia*, **1975**, 445–457.

Mayer, F. (1955). The pygmy sunfish. *Aquarium Journal*, **26**, 309.

Nicholson, A. J. (1954). An outline of the dynamics of animal populations. *Australian Journal of Zoology*, **2**, 9–65.

Root, R. B. (1967). The niche exploitation pattern of the blue-grey gnatcatcher. *Ecological Monographs*, 37, 317–350.

Rose, S. M. (1960). A feedback mechanism of growth control in tadpoles. *Ecology*, 41, 188–199.

Rubenstein, D. I. (1978). On predation, competition, and the advantages of group living. *Perspectives in Ethology*, 3, 205–232.

Rubenstein, D. I. (1981). Population density, resource patterning, and territoriality in the Everglades pygmy sunfish. *Animal Behaviour*, 29 (in press).

Schaffer, W. M. & Gadgil, M. D. (1975). Selection for optimal life histories in plants. *Ecology and Evolution of Communities* (Ed. by M. Cody & J. Diamond). Princeton Press, Princeton, N.J.

Scott, D. P. (1962). Effects of food quantity on fecundity of rainbow trout *Salmo gairdneri*. *Journal Fisheries Research Board of Canada*, 19, 715–731.

Sohn, J. J. (1977). Socially induced inhibition of genetically determined maturation in the platyfish, *Xiphophorus maculatus*. *Science*, 195, 199–201.

Solomon, D. J. (1977). A review of chemical communication in freshwater fish. *Journal of Fish Biology*, 11, 363–376.

Steinwascher, K. (1978). Interference and exploitation competition among tadpoles of *Rana utricularia*. *Ecology*, 59, 1039–1076.

Wilbur, H. M. (1976). Density-dependent aspects of metamorphosis in *Ambystoma* and *Rana sylvatica*. *Ecology*, 57, 1289–1296.

Wilbur, H. M. (1977). Density-dependent aspects of growth and metamorphosis in *Bufo americanus*. *Ecology*, 58, 196–200.

Wilbur, H. M. & Collins, J. P. (1973). Ecological aspects of amphibian metamorphosis. *Science*, 182, 1305–1314.

Yamagishi, H., Maruyama, T. & Mashiko, K. (1974). Social relation in a small experimental population of *Odontobutis obscurus* (Temminck et Schlegel) as related to individual growth and food intake. *Oecologia*, 17, 187–202.

Yu, M. & Perlmutter, A. (1970). Growth inhibiting factors in the zebra-fish, *Brachydanio rerio* and the blue gourami, *Trichogaster trichopterus*. *Growth*, 34, 153–175.