

SOCIAL EFFECTS IN GROWTH EXPERIMENTS. GROWTH OF JAGUAR GUAPOTE (*Cichlasoma managuense*) IN ISOLATION AND IN SMALL GROUPS

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ABSTRACT

The growth rate and feed conversion of juveniles of the jaguar cichlid (*Cichlasoma managuense*) are compared at constant densities, in groups of 2, 5, 10 and 20 individuals per aquaria, and as isolated individuals. Density had a positive correlation with heterogeneous growth (coefficient of variation), with mortality and with mean and maximum growth rates. Feed conversion correlated negatively with density. Marked adaptation effects were observed during the first phases of the experiment. These effects were much stronger in individual fishes than in fish groups and appeared to be inversely correlated with density. After adaptation the growth rate of biggest fishes in the groups is still significantly greater than that of individual fishes. It is concluded that heterogeneous growth is not only due to growth depression of subordinate fishes but also to growth enhancement of dominant fishes.

RESUMEN

Se evaluaron el crecimiento y la conversión alimenticia de juveniles de guapote tigre (*Cichlasoma managuense*) mantenidos a densidades constantes de 1, 2, 5, 10 y 20 individuos por pecera. La densidad mostró una correlación positiva con el coeficiente de variación (crecimiento heterogéneo), con la mortalidad y con las tasas de crecimiento promedio y máxima. La conversión alimenticia presentó una correlación negativa con la densidad.

Se observaron fuertes efectos de adaptación durante las primeras fases del experimento. Estos efectos fueron mucho más intensos en los peces aislados que en los peces en grupo y mostraron una relación inversa con la densidad. Después de la adaptación, la tasa de crecimiento de los peces más grandes de cada grupo fue significativamente mayor que la de los peces individuales. Se concluye que el crecimiento heterogéneo no se debe solamente a la reducción del crecimiento de los peces subordinados sino también a la estimulación del crecimiento de los peces dominantes.

INTRODUCTION

Laboratory and field experiments on fish growth are generally performed on groups of animals. The results are thus generally influenced by social effects on growth (JOBLING and REINSNES 1986). Growth can be inhibited or facilitated by social effects (NOAKES 1978). Territoriality and dominance are behaviours which may inhibit growth, especially in artificially crowded production or laboratory conditions. Recently, RUZZANTE (1994) has reviewed the various ways, by which competitive behaviour can affect growth: disproportional food acquisition as dominant fishes eat more than subordinates, stress effects in subordinate fish and disproportionate metabolic expenses, the last generally in subordinate fishes, but in some cases also in dominant ones. Social inhibition effects are particularly apparent in

aggressive fishes species, when confined into the restricted spaces of production or laboratory facilities. The result is heterogeneous growth of the group, called also growth depensation, characterized by the appearance of «shooters» (individuals with size well above average) or «stunts» (individuals with size well below average). Generally speaking, social competition is the cause of an inverse correlation between fish density and fish growth in most species (BACKIEL and LECREN 1978).

On the other hand, social behaviour has also advantageous effects in resource allocation and defense as has been described for fish schools (NOAKES 1978, KEENLEYSIDE 1979). Social facilitating effects have also been ascribed to the improvement of learning capabilities in the laboratory and to enhancement of feed consumption (OLLA and SAMET 1974, NOAKES 1978, WEATHERLEY and GILL 1987).

In laboratory experiments, designed to evaluate the growth potential of a fish species, these group effects are often neglected. The average growth is mostly taken as representative, but this growth is influenced by group effects, often in changing ways, since density, and thus the associated social effects, often decrease during an experiment because of mortality. If growth depensation occurs because inhibited individuals «consume less than a single isolated individual able to command the same food supply» (WEATHERLEY and GILL 1987), then should not the growth of shooters be more representative of the growth potential of the species? On the other hand, if shooters, because of social competition, eat more than they would as isolated individuals, should not growth better be tested on isolated individual fish, independently of social effects?

The jaguar cichlid (*Cichlasoma managuense*) is a well armed, piscivorous cichlid who builds up strong dominance hierarchies resulting in extremely different growth of «shooters» and «stunts» at high densities (BLEICK 1970, GÜNTHER 1988). In densities between 20 and 400 juveniles per aquarium of 45 l, GÜNTHER and GALVEZ (1992) found a negative correlation between density and mean growth, but not between density and the growth of shooters. They attributed

growth depensation to aggressive competition resulting in high mortality and disproportional food acquisition. The purpose of the present study is to compare the growth of juveniles of jaguar cichlid both in groups of low densities and as isolated individuals. In order to keep density constant, dead fishes were replaced daily by other fishes of similar weight.

MATERIALS AND METHODS

Fishes. A batch of about 500 juveniles was used, which were spawned and reared together in a 2000 liter tank in the laboratory. Before the start of the experiment the animals were acclimatized for 2 weeks in groups of 25 in the same 45 liter aquaria which were used for the experiment. They were 125 days old and weighed about 2 g at experimental begin.

Experimental design. At the begin of the experiment 115 juveniles of similar weight were distributed randomly into 16 aquaria of a battery with a recirculation water system. The aquaria were visually isolated from each other. Four aquaria were stocked with individual fish and 4 groups of 3 aquaria were stocked with 2, 5, 10 and 20 fish each. The remaining juveniles were kept in a second identical battery and used for substitution.

The experiment was run for 42 days. All fishes were individually weighed at days 0, 14, 28 and 42. Two or three times a day, the aquaria were checked for dead fishes. They were taken out immediately and weighed. Fishes of similar weight ($\pm 10\%$) were chosen from the remaining population and substituted into the experimental aquaria in the evening just before lights went out. During the second half of the experiment the substituted fishes were marked with three different small cuts into the pelvic or dorsal fin. Mark A was applied between days 12 and 20, mark B between days 21 to 29 and mark C between days 30 to 39 of the experiment.

Feed. The animals were fed a laboratory formulated high protein diet (GÜNTHER and BOZA 1991: protein 50%, lipid 15%, carbohydrate 15%). On the basis of a metabolic ration of 14 g feed/kg^{-0.8} fish weight/day and a feed conversion of 1.5 the daily feed was allocated. This ration was

found to be similar to *ad libitum* feeding of fish of this weight (GÜNTHER and GALVEZ 1992). The feed ration was recalculated every 14 days by using the real mean fresh weight.

Water quality. Temperature and dissolved oxygen were measured daily in the inflowing water, nitrite, pH and total ammonia every two weeks. Mean temperature during the experiment was 27.7° C (maximum 29.7, minimum 23.5), mean dissolved oxygen was 6.6 ppm (maximum 7.0, minimum 6.3). Nitrite was always below 0.02 ppm, total ammonia below 0.4 ppm and pH was between 6.6 and 7.1.

Data analysis. All fishes were individually weighed at days 0, 14, 28 and 42. The following data were calculated:

Fish in groups:

Wm mean weight of each repetition (aquarium)
 Wmax maximum weight of each repetition
 Wmin minimum weight of each repetition
 CV coefficient of variation of each repetition
 Gm mean growth coefficient G (see below)
 Gmax growth coefficient G of the biggest fish in each repetition
 Gmin growth coefficient G of the smallest fish in each repetition

Individual fish:

Mean weight of all 4 individuals
 FC feed conversion wet basis

The growth coefficient G was calculated as follows:

$$G = \frac{\sqrt[3]{W_f} - \sqrt[3]{W_i}}{t}$$

where W_i , f initial and final wet weight, t days of the period. This growth parameter is advantageous for comparative purposes because it changes little over short time periods (IWAMA and TAUTZ 1981, GÜNTHER *et al.* 1992).

The statistical analysis was by ANOVA, using the LSD test for comparing means. The

analysis was done with the software STATGRAPHICS. Mean values are reported with 95% confidence limits.

RESULTS

Growth versus density. The growth parameters calculated for the whole experimental period of 42 days are listed in table 1. At the beginning of the experiment mean, maximum and minimum weights are not statistically different between treatments, at the end of the experiment the mean and maximum weights were significantly higher at higher densities. The minimum weights were lowest at density 5, and still lower at densities 10 and 20 than at treatments 1 and 2. The growth coefficient G behaves accordingly: mean and maximum G increased with density, while the growth of the smallest fishes was lower at higher densities. The feed conversion decreased significantly with increasing densities.

The initial CV was similar in all treatments, albeit somewhat higher in the individual fishes. During the experiment the CV increased markedly at higher densities, reaching the highest value (52.3%) at density 5, while the CV of individual fishes hardly changed.

Growth versus duration of the experiment. Growth and feed conversion parameters did not remain stable during the three 14-day phases of the experiment. Feed conversion decreased and growth increased from the first to the last phase. In figure 1 the values of feed conversion of each treatment are plotted for each experimental period. The feed conversion decreased from begin to the end of the experiment in all treatments. The changes were particularly dramatic with the individual fishes. Table 2 shows the decrease of the feed conversion in multiples of the values of the first phase. The decrease appears to be less at the higher densities.

The growth coefficients G of average, maximum and minimum fishes of each treatment increased during the experiment. Table 2 shows the increase in growth coefficients for average, maximum and minimum fishes from the first to the last phase in multiples of the growth of the first

Table 1
Initial and final growth parameters

<i>Treat</i>	<i>Wmean_i</i>	<i>Wmax_i</i>	<i>Wmin_i</i>	<i>CV_i</i>	
1	2.19 a	2.19 a	2.19 a	9.66 b	
2	2.19 a	2.26 a	2.11 a	4.75 a	
5	2.17 a	2.42 a	2.00 a	8.53 ab	
10	2.21 a	2.48 a	1.98 a	7.83 ab	
20	2.18 a	2.44 a	1.90 a	7.41 a	

<i>Treat</i>	<i>Wmean_f</i>	<i>Wmax_f</i>	<i>Wmin_f</i>	<i>CV_f</i>	<i>FC</i>
1	3.97 a	3.97 a	3.97 cd	9.74 a	2.09 a
2	4.90 ab	5.72 b	4.08 d	18.55 b	1.89 ab
5	5.11 b	8.96 c	2.48 a	52.30 c	1.55 ab
10	5.60 b	9.11 c	3.39 b	32.12 b	1.39 b
20	5.90 b	10.14 c	3.45 bc	35.89 bc	1.32 b

<i>Treat</i>	<i>Gmean</i>	<i>Gmax</i>	<i>Gmin</i>	<i>Mort.</i>
1	0.075 a	0.075 a	0.075 b	0 a
2	0.094 ab	0.112 b	0.075 b	1.19 a
5	0.101 ab	0.173 c	0.022 a	1.59 a
10	0.113 b	0.175 c	0.059 b	6.35 b
20	0.122 b	0.195 c	0.064 b	5.36 b

W: fresh weight in g, CV: coefficient of variation, Mort.: mortality in %/day, G: growth coefficient, mean, max, min: average, maximum and minimum per repetition, i,f: initial, final values followed by the same letters are not different statistically, LSD-test 95%.

Table 2
Variation of feed conversion and of growth coefficient G from the first to the third experimental phase, expressed in multiples of the values of the first phase

<i>Treatment</i>	<i>FC</i>	<i>Gmean</i>	<i>Gmax</i>	<i>Gmin</i>
1	0.17 a	9.62 a	9.62 a	9.62 a
2	0.43 ab	2.93 b	3.19 b	11.51 a
5	0.42 ab	3.94 b	2.60 b	5.01 a
10	0.47 b	2.76 b	2.42 b	14.92 a
20	0.48 b	1.89 b	2.06 b	1.74 a

FC, Gmean, max, min: multiples of feed conversion and of growth coefficients of the first experimental phase. Values in each column sharing the same letter are not different statistically. LSD test 95%.

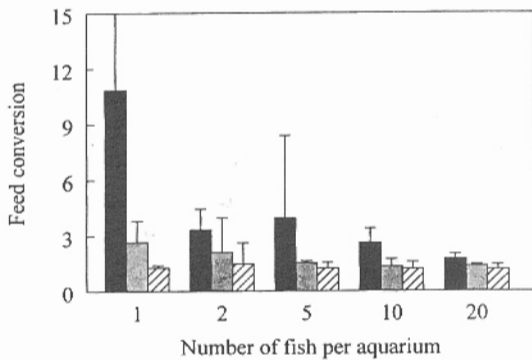


Figure 1. Feed conversions of densities 1 to 20 for each experimental 14-day phase. Black: first phase, gray: second phase, hatched: third phase. Error bars: 95% confidence limits.

phase. For mean and maximum G the increase is significantly higher in individuals than in the groups. Within the groups the increase in growth coefficient is apparently higher in low than in high densities, but the differences are not significant. There is no apparent relation between the increase in minimum G 's and density.

Mortality. In total 228 fish died during the experiment and were substituted by fishes of similar weight. The relative mortality was correlated with density, the highest values occurred in densities 10 and 20 (table 1). No fishes died in the individual treatment. In figure 2 the weights of all 228 dead

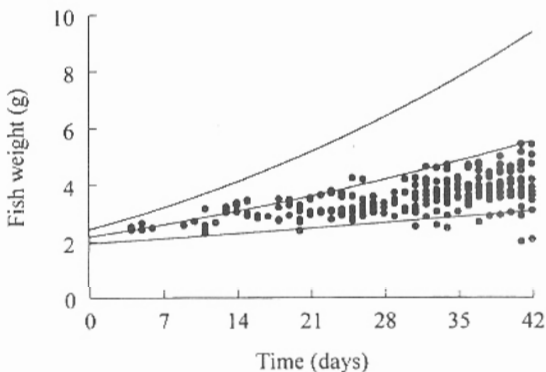


Figure 2. Weight of the dead fishes during the experiment. Lines are growth curves for maximum, mean and minimum growth coefficient G , calculated from the average of densities 5, 10 and 20.

fishes are plotted against the experimental period. The mortality increased during the experiment, with the highest daily mortality at the end of the experiment. For comparison growth curves calculated from mean, maximum and minimum growth coefficients taking the average of the densities 5, 10 and 20 are plotted. The weight of dead fishes was, with some exceptions, generally well below the mean growth curve. Marked fishes were more frequently killed than not marked ones. While the proportion of every mark out of the whole fish population was not more than 20%, in the first days after introduction the marked fishes made out more than 70% of fishes killed. In total 59% of fish marked A (20 out of 34), 82% of fish marked B (50 out of 61) and 77% of fish marked C (86 out of 112) were killed. Since fishes marked A and B were 3 and 2 times, respectively, longer in the experiment, the probability of marked fishes being killed increased to the end of the experiment.

DISCUSSION

The overall growth rate in this experiment (G_{mean} at density 20: 0.12) is well below the value obtained by GÜNTHER and GALVEZ (1992) with the same density (0.18, recalculated), while feed conversions were very similar (1.32 resp. 1.39). However, if we compare only the growth values of the third experimental phase, they appear to be quite close together (0.17 vs. 0.18). Obviously, the overall growth rate was impaired in this experiment by adaptation effects during the first experimental phases (see below).

In the fish reared in groups the phenomenon of heterogeneous growth was well marked. The coefficient of variation at the end of the experiment was much greater at the higher densities (5, 10 and 20) than in densities of 2 or in individual fishes. «Shooters» and «stunts» became rapidly apparent in group reared fishes. While the growth of «shooters» was positively correlated with density (table 1), the growth of «stunts» was smaller at higher densities. The growth coefficient of «shooters» during the last phase (0.27) is even higher than the G_{max} obtained by GÜNTHER and GALVEZ (1992) at the same density of 20 (0.24, recalculated).

Although fish in this experiment were adapted for two weeks to the experimental setup in groups of 25, at the begin of the experiment group composition and density was changed, and some fishes were even individually isolated. All fishes showed a marked adaptation period during the first phases of the experiment, during which growth was depressed and the feed conversion much higher than afterwards. The adaptation stress was much more severe with individual fishes than with fish held in groups, and was also stronger at lower than at higher densities (table 2). However, in the third growth phase all fishes were well adapted, since there are no differences in feed conversion between treatments in this phase. Thus it appears that group rearing facilitates the initial adaptation to a new social arrangement and that individual fishes are disproportionately affected by isolation. Similar observations were reported by WICKINS (1985) and KNIGHTS (1987).

When we compare the growth rates during the third experimental phase, when all fishes were well adapted, it appears that the growth rate of «shooters» was significantly greater and that of «stunts» significantly smaller than the growth rate of individual fishes (figure 3). Thus growth depensation cannot be attributed only to reduced feed consumption by the «stunts» (WEATHERLEY and GILL 1987), but must be attributed also to increased feed consumption by «shooters», which must have consumed more than they would as isolated individuals. Social competition thus not only inhibits subordinates, but also stimulates «shooters» to more growth. Thus, while the maximum growth potential is attained by competitive «shooters», the «normal» growth rate of the jaguar guapote is better assessed at isolated, well adapted individuals.

While GÜNTHER and GALVEZ (1992) obtained a significant negative correlation between mean growth rate and density (at densities between 20 and 400 per aquarium of 45 l), in this experiment both mean and maximum growth rates were higher at the higher densities. Social factors showed both facilitating (adaptation to a new social situation, enhanced feeding of «shooters») and inhibiting (prevention of «stunt» feeding) effects. At higher densities the proportion of «stunts» will increase

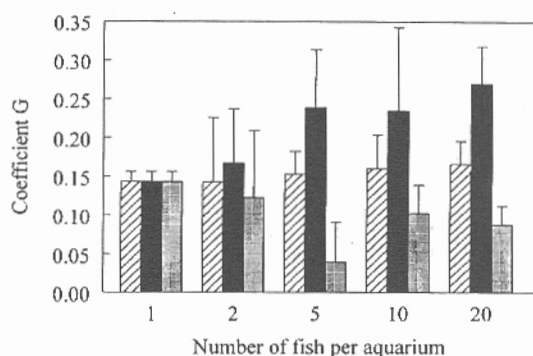


Figure 3. Growth coefficients G in the last experimental phase. Hatched: G mean, black: G max, gray: G min. Error bars: 95% confidence limits.

disproportionately and thus depress mean weight and mean growth. In our experimental conditions the density of 20 juveniles per aquarium seems thus to provide the best tradeoff between social facilitation and social inhibition effects on the growth of guapote tigre juveniles.

In most growth experiments where mortality occurs, this mortality will obviously affect mean weight and thus growth assessment. In our experiment the growth parameters were not influenced by mortality as dead fishes were substituted immediately by fishes of similar weight.

Mortality was clearly due to aggressive attacks, as could be inferred from severe bite damages observed in dead fishes (GÜNTHER and GALVEZ 1992). With some exceptions, mainly fishes belonging to the lower weight classes were killed (figure 2). Mortality was clearly related to fish density and to the duration of the experiment. The increase during the experiment may reflect the ongoing adaptation of the fish to the experimental conditions. While care was taken to introduce substituted fishes at night just before lights went out, most marked fishes were killed within a few days after introduction. The mortality of marked fishes increased towards the end of the experiment. This may reflect an increased individual recognition, as stable dominance hierarchies develop or behavioural recognition of the stressed, recently introduced individuals.

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