UNICIENCIA 9
pp. 33-39
1992

THE EFFECT OF HIGH REARING DENSITIES ON THE GROWTH OF JUVENILES OF THE CICHLID, *Cichlasoma managuense* (GÜNTHER, 1869)

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RESUMEN

Se investigó el efecto del cultivo en alta densidad sobre la tasa de crecimiento de juveniles de guapote tigre. Mientras que la tasa de crecimiento promedio disminuye con la densidad, el crecimiento de los peces más grandes no resultó afectado. Con altas densidades de cultivo, el crecimiento promedio disminuye tanto debido a un mayor grado de enanismo en los individuos pequeños, como a que aumenta su cantidad relativa. El coeficiente de asimetría resulta ser un mejor indicador de los efectos competitivos que el coeficiente de variación. Se concluye que por lo menos en aguas estancadas, las altas densidades no afectan la jerarquía de dominancia que se forma entre individuos de guapote tigre.

ABSTRACT

The effect of high density culture on the growth of juvenile jaguar cichlids was investigated. Mean growth rate decreased with density, while the growth rate of the largest fishes was not affected. Reduction in mean growth resulted from a greater number of stunted individuals as well as from a higher degree of stunting. Skewness appears to be a better indicator of competitive effects than the coefficient of variation. It is concluded that at least in stagnant waters, even high densities do not affect the strong dominance hierarchy which establishes among guapote juveniles.

INTRODUCTION

While high-density culture offers obvious economic advantages, a limit is soon reached as the growth rate of most cultured fish species is negatively correlated with density. Density-dependent competition causes an increase of growth variation and positive skewness in weight distribution, hence reducing mean growth. In aggressive species high mortalities and even cannibalism occur at high densities (for examples and discussion see Backiel and Lecren 1978, Noakes 1978, Backiel 1985, Jobling 1985, Doyle and Talbot 1986, Jobling and Reinsnes 1986, Knights 1987, Davies and Olla 1987, Katavic et al. 1989).

However, in some salmonid species, no correlation between growth rate and density or even a positive one has been reported (Soderberg et al. 1987, Soderberg and Meade 1987, Wallace et al. 1988). At high densities the hierarchical and/or territorial social structure will break down, reducing levels of aggression and hence competition (cf. Li and Brocksen 1977, Jobling and Reinsnes 1986, Knights 1987, Wallace et al. 1988). In consequence, very high culture densities have been recommanded to overcome competition effects (Seymour 1984).

The jaguar cichlid *(Cicklasoma managuense)* (Günther, 1869) (local names: guapote tigre, guapote barcino) is a Central American, piscivorous cichlid ranging from Costa Rica to Honduras. In Nicaragua the guapote barcino is a very common market fish (Barlow 1976), in Costa Rica it is appreciated in rural river fishing because of his excellent taste and sport fish qualities. Because it is well adapted to high temperature and low oxygen levels, the guapote tigre has been

Table I

Parameters of water quality
Means of the whole period

Density Fish/aq.	*Waterflow l/min*	*Oxygen mg/l*	*Temperature °C*	*NH_3 (total) mg/l*	*NO_2^- mg/l*	*NO_3^- mg/l*
20	1.4	5.35	28 ± 0.63c	< 1	< 0.5	< 100
50	1.8	4.95_a				
100	2.2	4.84_a				
200	3.2	4.63_b				
400	4	4.59_b				

a, b: treatment means of oxygen are significantly different except those with the same suffixes (Student T-tests), c: 95% confidence limits.

recommanded for recruitment control in extensive tilapia culture (Dunseth and Bayne 1977, Lovshin 1982).

The guapote tigre is an aggressive and well armed species (Bleick 1970). When culturing fry at intermediate densities (0.25 individuals/liter) aggression becomes evident after one month of life and causes significant mortality (Günther 1988). In this paper we test the hypothesis that very high densities could reduce the aggressive behaviour and hence improve growth and reduce mortality in guapote juveniles.

MATERIAL AND METHODS

More than two thousand (2326) full siblings of guapote tigre, previously grown together in a 2000 liter tank, were used. They were stocked in the aquaria at an age of 41 days with an average weight of 0.5 g. and acclimatized for a period of 14 days in the experimental facility prior to the start of the experiment.

The experimental facility was a 16-aquaria-mannifold (aquarium volume: 45 liter) connected to a recirculating water system including pump, heaters, settlers, biological filters and oxygenation column. For every aquarium the water flow could be adjusted up to 5 l/min, and was increased about 3 times from low to high densities in order to minimize differences in water quality (see Table I). Faeces and feed rests were removed twice daily (6 a.m. and 6 p.m.). Light period was from 6 a.m. to 8 p.m. Oxygen was measured twice daily (6 a.m. and 6 p.m.) in each aquarium. In the outcoming water, temperature was taken daily and ammonium, nitrite and nitrate twice weekly. In addition to feeding times, the behaviour of the fishes was observed daily between 5 and 6 p.m.

A completely randomized design was used, with 5 triplicate treatments (20, 50, 100, 200 and 400 fishes per aquarium).

The feed was a commercial dry diet (Trouvit 1) with grain diameter between 1-2 mm. (protein 52% min, humidity 11% max, fibre 11% max, lipids 8,5% min, minerals 11% max). According to previous experiences a feeding level of 20 g/Kg^0,8/day was employed and adjusted at 14 day intervals in order to ensure feeding «at libitum» and to reduce competition. Feed was given 5 times daily except during weekends (3 times).

All fishes were counted and weighed at days 0, 14, 28, 42 and 56 of the experiment, except at days 0 and 14 for the densities of 200 and 400, where only 25% samples of each replication were taken. The following 9 variables were calculated at 2-week intervals for every repetition (W: mean fish weight of each repetition, N: number of fishes per aquarium, i,f: initial,final of 2-week periods):

Mean weight:

$MW = EXP((LN\ Wi + LN\ Wf)/2)$

Density (D, as mean number of fishes per aquarium):

$D = EXP((LN\ Ni + LN\ Nf)/2)$

Mean growth rate:

$SGRm = ((LN\ Wf - LN\ Wi)/14) \times 100$

Maximum growth rate:

SGRmx : as above, but taking the mean weight of the three heaviest fishes per repetition.

Feed conversion:

$FC = Feed\ amount(dry)/((Wf-Wi) \times ((Ni+Nf)/2))$

Mean coefficient of variation:

$CV = (CVi + CVf)/2$

Mean coefficient of asymmetry (Skewness):

$SK = (SKi + SKf)/2$

Mortality:

$M = ((Ni - Nf)/Ni) \times 100$

The data were analyzed by a standard multiple regression analysis (Tabachnick and Fidell 1983) taking the natural logarithms of the first 2 variables (MW and D) as independent variables (correlation coefficient between them = -0,25) and the last seven (SGRm, SGRmx, SGRmn, FC, CV, SK and M) as dependent variables. The analysis was run on STATGRAPHICS software.

RESULTS GROWTH

Table II shows initial and final values of the analyzed variables for each treatment. Mortality varied between 18% and 37% and was not related to density. The average mean weight of all fishes increased from initially 0.43 g. to 4.53 g. after 8 weeks. The average weight of the 3 biggest fishes per repetition increased from 0.68 to 12.9 g. and the average weight of the three smallest fishes per repetition increased from 0.22 to 1.54 g. in the same period (Fig. 1). The coefficient of variation increased from about 29% to 63%, while the coefficient of asymmetry increased from 0.7 to about 1.8 (Fig. 2). For the whole period, the mean specific growth rate, the maximum specific growth rate fand the minimum specific growth rate were 4.1, 5.3 and 3.4% BW/day respectively, while the mean feed conversion was 1.7.

Table III shows the results of the standard multiple regression analysis of seven dependent variables (SGRm, SGRmx, SGRmn, FC, CV, SK and Mortality) on the logarithms of mean weight and density.

The mean specific growth rate (SGRm) of all treatments decreased from 5.4% BW/d in the first 2 week period to 2.42% BW/d in the last. SGRm was significantly negatively correlated with both mean weight and density, which together explain about 84% of the variability.

The mean maximum growth rate (SGRmx)

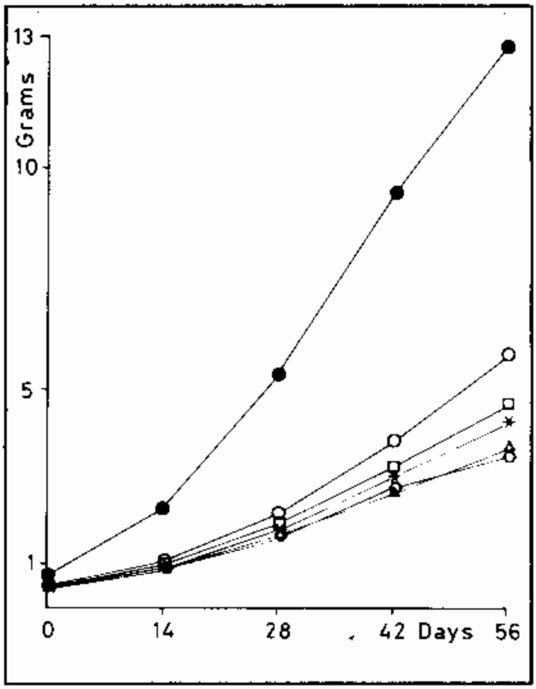

Fig. 1. Weight increase of fishes over the experimental period. Filled circles: pooled data for the 3 heaviest fishes per repetition. Circles, squares, stars, triangles and hexagons show the mean weight for treatments 20, 50, 100, 200 and 400 fishes per aquarium.

Table II

Growth parameters. Mean values over the whole period

Ni	*Nf*	*Wi* *g*	*Wf* *g*	*Wmxi* *g*	*Wmxf* *g*	*Wmni* *g*	*Wmnf* *g*
20	13.7	0.46	5.75	0.65	10.77	0.26	2.54
50	41	0.45	4.61	0.64	13.32	0.25	1.68
100	77	0.44	4.20	0.68	13.31	0.19	1.32
205	152	0.41	3.62	0.75	12.83	0.22	1.08
400	251.7	0.41	3.47	0.67	14.08	0.18	1.10

SGR	*SGRmx* *%W/d*	*SGRmn* *%W/d*	*FC* *%W/d*	*M*	*CVi* *%*	*CVf*	*SKi*	*SKf*
4.51	5.01	4.07	1.39	31.5	32.2	57.8	0.8	1.06
4.15	5.42	3.4	1.61	18.0	28.7	70.8	0.9	1.61
4.03	5.31	3.46	1.74	23.0	30.0	64.1	0.53	1.90
3.89	5.11	2.84	1.83	25.9	27.2	61.4	0.84	2.15
3.82	5.44	3.23	1.88	37.1	27.0	62.4	0.27	2.40

i, f: initial, final, W: mean weight, mx, mn: 3 biggest, 3 smallest fishes per repetition, SGR: mean specific growth rate, N: number of fishes per aquarium, FC: apparent feed conversion, M: mortality, CV: coefficient of variation, SK: coefficient of asymmetry.

decreased from 7.68% BW/d in the first 2 weeks to 2.9% BW/d in the last two. There is a strong negative correlation with mean body weight, which explains alone 71% of the variability, but no significant correlation with density.

The mean minimum growth rate (SGRmn) decreased from 4.42% BW/d in the first 2 week period to 1.94% BW/d in the last. The minimum growt rate is negatively correlated with both body weight and density, but with a very low determination coefficient (0.31).

Mean feed conversion (FC) increased from

Table III

Multiple regression analysis

Dependent variables	*Const.*	*B1 (LN MW)*		*B2 (LN D)*		*R^2*	*F*
SGRm	6.5985	-1.6739**	(0.83)	-0.3912**	(0.11)	0.84	154.6**
SGRmx	6.9724	-2.5939**	(0.71)	-0.1051 NS	(0.002)	0.73	80.6**
SGRmn	6.1529	-1.5308**	(0.31)	-0.4629*	(0.07)	0.31	14.1**
FC	0.2770	0.6006**	(0.45)	0.2557**	(0.19)	0.53	32.1**
CV	33.916	15.1596**	(0.75)	1.4660*	(0.02)	0.75	90.6**
SK	0.3827	0.4806**	(0.35)	0.2015**	(0.15)	0.40	20.5**
M	2.0366	3.1348*	(0.1)	0.9227 NS	(0.02)	0.11	3.6*

NS: non significant, *, **: $P<0.05$, $P<0.01$, ( ) squared semipartial correlations give the contribution of each independent variable to the correlation coefficient of the whole regression. R^2 and F refer to the whole regression.

a mean of 1.31 in the first two weeks to 2.46 in the last period of 2 weeks. There is a significant positive correlation of the feed conversion with both body weight and density, but with a low determination coefficient however (53%).

Both distribution indices (CV and SK) were positively correlated with mean weight and density. The determination coefficient is much higher for CV (75%), which depends much more on body weight than on density. While showing higher variability (r^2 40%) the SK has a relative strong dependence from density (Fig. 2).

The mortality over the whole period was not dependent on density, and shows only a small dependence on body weight. While the full regression is still significant ($P<0.05$), both independent variables explain only 11% of the mortality. This could be expected, since the mortality increased during the first 42 days, but then declined without relation to density (Fig. 2).

BEHAVIOUR

From the very beginning a dominance hierarchy built up in each aquarium. During the first two weeks the fishes occupied —when undisturbed— homogenously the entire aquarium volume, maintaining the distances by constant attacks between neighbours. The bigger fishes became rapidly dominant and could be easily recognized visually by their light coloration in contrast to subordinate, dark individuals (Bleick 1970, Günther 1988).

In the second two-week period the dominant fishes began to claim greater areas, preferentially at the aquarium bottom, where they defended uneaten feed rests, rushing however first of all to surface at feeding time. Subordinate fishes were progressively cornered into smaller aquarium areas, and they gradually ceased to rush to feed together with the dominants. However, a considerable degree of aggression still persisted among subordinate fishes.

During the last weeks, in all high density aquaria, subordinate fishes agglomerated into dark, dense clusters in corners, with the peripheral fishes trying incesantly to get into the center. At feeding time only few subordinates competed directly with the dominants.

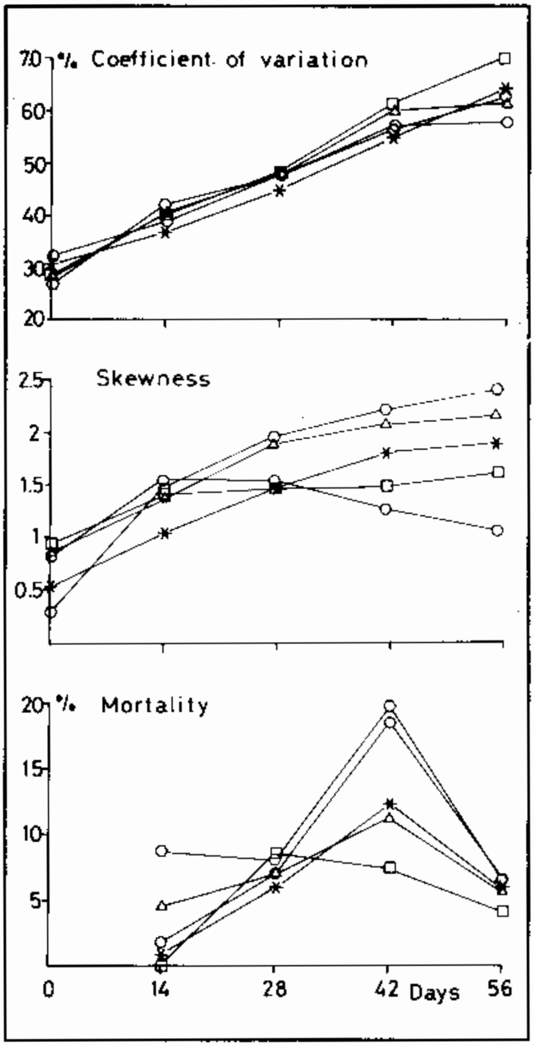

Fig. 2. Change of the coefficients of variation, skewness and mortality over the experimental period. Simbology as in Fig. 1.

Mortality by aggression was greatest in the third 2-week period, decreasing again afterwards. Most dead fishes were severely damaged on fins and flanks, with scales and even skin being bitten off. Cannibalism was first observed after 4 weeks, when the biggest fishes were be observed while partially swallowing smaller ones (Günther 1988). Cannibalism increased steadily until the end of the experiment. During the last 2-week period, about 50% of the mortality was due to cannibalism.

DISCUSSION

In this experiment heterogenous growth was very marked. The coefficient of variation (CV) of the weight data, increased from around 30% to over 60% in 8 weeks, showing however almost no dependence on density. On the other hand, the skewness, which expresses asymmetry of weight distribution, increased from around 0.7 to a mean of 1.8, both being positively correlated with body weight and density. Therefore, skewness appears to be a better indicator of competition effects than CV, while showing however a greater degree of variability (less predictability) than the CV (Fig. 2).

All three growth rates measured (mean, maximum and minimum) decreased during the experiment, being negatively correlated with body weight. However, in contrast to both mean and minimum growth rates, the maximum growth rate (SGRmx) was not correlated with density. Apparently, the growth of dominant fishes was not impaired by the amount of other fishes around them. As there are no differences in the heaviest fishes, the reduction in mean growth rate at higher densities must be due to a greater number of stunted individuals (as may be inferred from increasing SK) (Rose 1960 in Doyle et al. 1986), but also because subordinates are more stunted at higher densities. This is demonstrated by the density dependence of the minimum growth rate.

Causes for heterogenous growth in aquatic animals can be environmental, genetic or social (Ra'Anan et al. 1984). In the present experiment, environmental effects can be excluded since the conditions in all treatments were very similar. It is thought that the differences in oxygen were too small to have a major effect on growth. Genetic effects (for example growth differences between males and females), may have been present, but apply equally to all treatments. Other causes, like a chemical «stress»-factor (Henderson-Arzapalo 1980) seem improbable, since in this case a density dependent effect on the maximum growth rates should be apparent.

In consequence, heterogenous growth in the guapote appears to be caused mainly by aggressive competition. Continuous attacks between neighbours, preventing moving and feeding, could be observed regularly. Since in the last weeks most subordinate fishes did not even try to feed, severe intimidation appears to be the main mechanism of competition. Learning effects are probably important at this level (Knights 1987) and are facilitated by the conspicuous pale coloration of the few dominant individuals. In concordance with Koebele (1985), disproportional food adquisition appears to be the main cause for heterogenous growth.

While cannibalism increased throughout the experiment, mortality by aggression decreased again in the last weeks (Fig. 2). It is thought that most aggression mortality is caused by the continuous attacks between the subordinate fishes themselves. However, this type of behaviour decreased during the last weeks, when intimidation by dominants reached its maximum level and subordinate fishes aggregated into dense clusters.

Mortality by aggression and cannibalism will have different effects on the mean growth rate and on skewness. Because mainly small individuals die, the mean weight increases and skewness decreases. On the other hand, cannibalism may increase mean weight through a faster growth of the big animals because of a higher nutritional value of prey fish compared to a dry diet (Giles et al. 1986). However, in that case, skewness will increase as well. In the present study it is not possible to assess the relative importance of these effects, but it is probable that they obscured the density dependence of mean weight and growth rates.

Contrary to what has been reported for some salmonids, the results of the present study show that high density culture of *Cichlasoma managuense* will not smooth out the effects of the dominance and aggression. Genetic differences between fish species may explain this contradiction, but perhaps also differences in the culture conditions may be important: Salmonids are cultured mainly in race-ways, where forced swimming activity probably reduce aggressive interactions. As such, the effects of water movement on the aggressive interactions of the guapote could still be assessed.

ACKNOWLEDGMENTS

This study was supported in part by a grant of the Dutch Government to the project UNA/LUW/Acuacultura, an inter-university cooperation programme with the Department of Fish Culture and Fisheries (DFCF) of the Wageningen Agricultural University, The Netherlands. The authors thank Drs. J. Verreth and M. Verdegem of DFCF for revision of the manuscript and helpful comments.

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