FOOD DEPRIVATION AND COMPENSATORY GROWTH IN JUVENILE PIAVA, *Leporinus obtusidens*

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ABSTRACT

The growth and body composition of *Leporinus obtusidens* juveniles (32.0 ± 8.0 g; 137.3 ± 11.9 mm) were evaluated under food deprivation followed by refeeding. Fish were stocked in 130-L tanks (15 fish $tank^{-1}$), maintained at 26.6 ± 0.3 °C, and fed commercial feed (42% crude protein). Four feeding regimes (days fed to apparent satiation × days without food) were evaluated: control (144F:0D), 1D (1F:1D), 6D (6F:6D) or 12D (12F:12D). The greatest increase in weight and growth rates was observed in control. Fish in 1D, 6D or 12D grew to 73, 64 and 65% in weight of fish in control treatment, respectively. Total daily food intake was lower in 12D (1.02 ± 0.06 g) compared to control (1.28 ± 0.02 g). Water content of body composition was higher in control, but other parameters were not significantly different. *Leporinus obtusidens* showed partial compensatory growth, and the pattern of productive performance and final body composition could be adjusted to lipostatic model, since during food deprivation energy reserves are mobilized to maintain metabolism, resulting in weight loss, whereas during refeeding nutrients are used for restoration of energy reserves, slowing growth.

Keywords: fasting; hyperphagia; lipostatic model; refeeding

PRIVAÇÃO ALIMENTAR E CRESCIMENTO COMPENSATÓRIO EM JUVENIS DE PIAVA, *Leporinus obtusidens*

RESUMO

O crescimento e a composição corporal de juvenis de *Leporinus obtusidens* (32,0 ± 8,0 g; 137,3 ± 11,9 mm) foram avaliados em condição de privação alimentar seguida por realimentação. Os peixes foram estocados em tanques de 130-L (15 peixes $tanque^{-1}$), mantidos em 26,6 ± 0,3 °C e alimentados com ração comercial (42% de proteína bruta). Quatro regimes de alimentação (dias de alimentação até a saciedade × dias sem alimentação) foram avaliados: controle (144F:0D), 1D (1F:1D), 6D (6F:6D) ou 12D (12F:12D). O maior crescimento em ganho em peso e taxa de crescimento foi no controle. Os peixes dos tratamentos 1D, 6D e 12D cresceram 73, 64 e 65% do peso dos peixes do tratamento controle, respectivamente. O consumo alimentar diário total foi menor em 12D (1,02 ± 0,06 g) quando comparado ao controle (1,28 ± 0,02 g). A umidade da composição corporal dos peixes foi maior no controle, mas os demais parâmetros não foram significativamente diferentes. *Leporinus obtusidens* apresentou crescimento compensatório parcial, e seu padrão de desempenho produtivo e a composição corporal final poderiam ser ajustados ao modelo lipostático, no qual se prevê que durante a privação alimentar, as reservas energéticas são mobilizadas para a manutenção do metabolismo, resultando em perda de peso, enquanto na realimentação a alocação dos nutrientes é utilizada na restauração das reservas energéticas, diminuindo a velocidade de crescimento.

Palavras chave: hiperfagia; jejum; modelo lipostático; realimentação

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INTRODUCTION

The growth of some animal species is more rapid during recovery phase from partial or total food deprivation, compared to periods of continuous feeding (METCALFE and MONAGHAN, 2003). This more rapid growth allows these 'reduced growth' animals to reach a size similar to animals that did not undergo food restriction. This accelerated response, among individuals of same species and age which tends to restore the growth trajectory, is called compensatory growth or growth recovery (HECTOR and NAKAGAWA, 2012).

Dietary restriction and compensatory growth have been topics of great interest for considerable time (OSBORNE and MENDEL, 1915; JACKSON, 1937; WILSON and OSBOURN, 1960; DOBSON and HOLMES, 1984; JOBLING and JOHANSEN, 1999; ALI *et al*., 2003; JOBLING, 2010; ABOLFATHI *et al*., 2012), mainly because they concern issues related to differential growth of some animals compared to the rest of their species.

It is recognized that the size of an adult animal affects its life cycle, and for many species, a larger size positively influences aspects such as female fecundity, sexual selection, survival and population perpetuation (BLANCKENHORN, 2005). Therefore, animals with a slow developmental growth tend to be disadvantaged if they reach adulthood with a reduced size.

For compensatory growth to occur, it is necessary that animal possesses feedback mechanisms that guarantee that particular anabolic requirements, such as protein synthesis and glycogen formation are met (JOBLING and JOHANSEN, 1999; HORNICK *et al*., 2000; SKALSKI *et al*., 2005; PICHA *et al*., 2008).

Compensatory growth occurrence evidence has been obtained mainly from experimental studies, because field observational studies in this area are extremely rare (CARLSON *et al*., 2004; GAGLIANO and MCCORMICK, 2007). Most experimental studies on confined species have been performed to evaluate the use of compensatory growth in improving production and/or to influence the final product composition (GAYLORD and GATLIN, 2001; ALI *et al*., 2003; JIWYAM, 2010; YILMAZ and EROLDOGAN, 2011).

Leporinus obtusidens, popularly known as piava, belongs to Anostomidae family and occurs in watersheds that form La Plata River and in the South and Southeastern regions of Brazil (HARTZ *et al*., 2000). This species is omnivorous and its diet is mainly composed of seeds, aquatic insects, crustaceans and mollusks (HARTZ *et al*., 2000). Piava is valuable in fishing, mainly for its size in adulthood and for the taste of its flesh. Furthermore, *L. obtusidens* is used in fish culture, since it is well accepted in market, requires a low consumption of dietary protein and is easily handled (REYNALTE-TATAJE and ZANIBONI-FILHO, 2010).

Considering that information relating to food deprivation and compensatory growth in tropical and subtropical fish species is scarce, especially for omnivores, and that compensatory responses are species-specific, this study aimed to evaluate compensatory growth and body composition of *L. obtusidens* juveniles subjected to periods of food deprivation.

MATERIAL AND METHODS

The study was conducted with 180 juvenile *L. obtusidens*, which had a mean total weight and length of 32.0 ± 8.02 g and 137.3 ± 11.9 mm, respectively.

Fish were stocked in 12 circular fiber tanks (diameter = 0.75 m) with a capacity of 130 L, maintained with a minimum flow of 4.5 L min^{-1} and connected to a recirculating system with mechanical and biological filtration. The density used was 15 fish per experimental unit.

Fish were acclimated to experimental units for 30 days, and then were weighed and measured to record its initial size. During acclimation and experimentation, a commercial diet (3,400 kcal kg^{-1} energy, 9.0% ether extract, 1.5% phosphorus and 12% moisture) containing 42% crude protein (pellet size = 2 mm) was used.

Photoperiod was adjusted to 12 h light: 12 h dark, and water quality was measured weekly. The concentration of dissolved oxygen and total ammonia, pH and water temperature showed a mean (± standard deviation) of 6.37 ± 0.5 mg L^{-1}, 0.25 ± 0.14 mg N-NH_4^++NH_3 L^{-1}, 6.07 ± 0.13 and 26.62 ± 0.3 °C, respectively.

The experiment was conducted in a completely randomized experimental design with three replications for 144 days. Fish were subjected to four feeding regimes, that alternated periods of feeding to apparent satiation (F) with days of food deprivation (D): control (144F:0D), 1D (1F:1D), 6D (6F:6D) or 12D (12F:12D). Fish were fed to apparent satiation twice daily (10:00 h and 16:00 h), according to the feeding regime of each treatment. Feeding regimes were determined from available literature concerning complete compensatory growth, evidence of hyperphagia or adaptive changes in feeding habits (ALI and WOOTON, 2001; NIKKI *et al*., 2004).

At experiment beginning initial body composition was obtained from the analysis of ten fish. Biometric measurements were taken every 24 days for fish anesthetized with 200 mg L^{-1} Eugenol©; fish were individually weighed on a digital scale (0.01 g) and measured in an ichthyometer (0.01 cm). At the end of the experiment, three fish were sampled from each experimental unit for measuring liver weight, intestine length and for body composition analysis. Whole fish were stored at -20 °C until analysis.

The following performance parameters were evaluated:

- weight gain: WG (g) = final weight (g) – initial weight (g);

- specific growth rate: SGR (%) = 100 × [ln final weight (g) – ln initial weight (g)]/experimental period;

- Fulton's condition factor: K = 100 × [weight/(total length)^3];

- daily food intake: DFI (%) = 100 × [total food consumed (g)/(initial weight (g) × experimental period)];

- feed conversion: FC = food supplied (g)/weight gain (g);

- protein retention coefficient: PRC (%) = 100 × [(final weight × final body protein) – (initial weight × initial body protein)]/(food consumed × crude protein consumed).

In addition, the following biological indices were obtained:

- intestinal coefficient: IC = intestine length/total body length;

- hepatosomatic index: HSI (%) = 100 × [weight of liver tissue (g)/body weight (g)];

- visceral fat index: VFI (%) = 100 × [visceral fat weight (g)/body weight (g)].

For body composition analysis methods described in AOAC (1999) were used. Dry matter was determined gravimetrically after drying at 105 °C, whereas protein content was estimated by Kjeldahl method (N × 6.25) after acid digestion. Lipid levels were analyzed using Soxhlet method following ether extraction, and ash was determined by incineration at 550 °C in a muffle furnace.

Linear regression or ANOVA (ZAR, 2009) were used to assess the influence of food deprivation on growth. Normality and homoscedasticity were tested by Shapiro-Wilk and Levene tests, respectively, and angular transformation was applied to data expressed as a percentage. Where necessary, Tukey test was used to determine differences between mean values. All analyses were performed using GraphPad Software 4.03.

RESULTS

Performance parameters and biological indices in the rearing of juvenile *L. obtusidens* subjected to alternating regimes of food deprivation and refeeding are presented in Table 1.

Survival rate was the same ($P>0.05$) and very high in all treatments, since virtually no mortality was recorded.

Fish in food deprived treatments presented the same growth, whereas higher final weight and length were registered in control ($P<0.05$). Fish subjected to regimes 1D, 6D or 12D grew 73%, 64% and 65% of the weight registered in control treatment, respectively. Specific growth rate was higher in control fish, whereas no significant difference was found between other treatments.

During experiment, total weight and length of piavas were dependent on food deprivation (Figure 1). Highest growth rates were registered in control ($P<0.05$) and comparing only 1D, 6D and 12D treatments, no difference was detected between growth rates in terms of total weight or length until day 72 (P<0.05). Following this time, fish in treatment 1D showed a faster growth rate.

All treatments present the same condition factor at the end of the experiment (Table 1), however, higher values were recorded on days 24 and 120 for control fish (Figure 2).

Table 1. Performance parameters and biological indices (mean ± SD) of juvenile *Leporinus obtusidens* subjected to four cyclic feeding regimes (days fed to apparent satiation × days without food): control (144F:0D), 1D (1F:1D), 6D (6F:6D) or 12D (12F:12D) after 144 days. Different letters in each line indicate significant differences (P<0.05).

Parameter/Index	Feed regime			
	Control	1D	6D	12D
Survival (%)	97.8 ± 3.9	95.7 ± 3.9	100.0 ± 0.0	100.0 ± 0.0
Initial weight (g)	32.2 ± 9.73	32.5 ± 6.8	31.7 ± 7.3	31.5 ± 8.2
Final weight (g)	119.9 ± 5.61^{a}	87.5 ± 6.10^{b}	77.2 ± 5.58^{b}	78.5 ± 6.94^{b}
Weight gain (g)	87.61 ± 5.99^{a}	54.79 ± 5.91^{b}	45.48 ± 4.66^{b}	47.04 ± 4.13^{b}
Initial length (g)	137.0 ± 1.00	137.0 ± 1.20	138.0 ± 2.08	137.1 ± 1.58
Final length (g)	216.7 ± 1.60^{a}	198.0 ± 5.71^{b}	189.5 ± 3.11^{b}	191.0 ± 2.41^{b}
Specific growth rate (%)	0.91 ± 0.04^{a}	0.68 ± 0.04^{b}	0.61 ± 0.03^{b}	0.63 ± 0.04^{b}
Condition factor	1.18 ± 0.03	1.12 ± 0.02	1.14 ± 0.03	1.12 ± 0.02
Daily food intake (%)	1.28 ± 0.02^{a}	1.13 ± 0.14^{ab}	1.09 ± 0.07^{ab}	1.02 ± 0.06^{b}
Feed conversion	1.60 ± 0.04	1.79 ± 0.28	1.89 ± 0.11	1.72 ± 0.07
Protein retention coefficient (%)	29.67 ± 4.32	27.66 ± 3.89	26.92 ± 2.34	29.55 ± 3.28
Intestinal coefficient	0.88 ± 0.06	0.80 ±0 .03	0.83 ± 0.07	0.83 ± 0.11
Hepatosomatic index (%)	1.11 ± 0.25	1.18 ± 0.16	1.08 ± 0.25	1.05 ± 0.13
Visceral fat index (%)	1.82 ± 0.58	1.37 ± 0.28	1.40 ± 0.63	1.33 ± 0.66

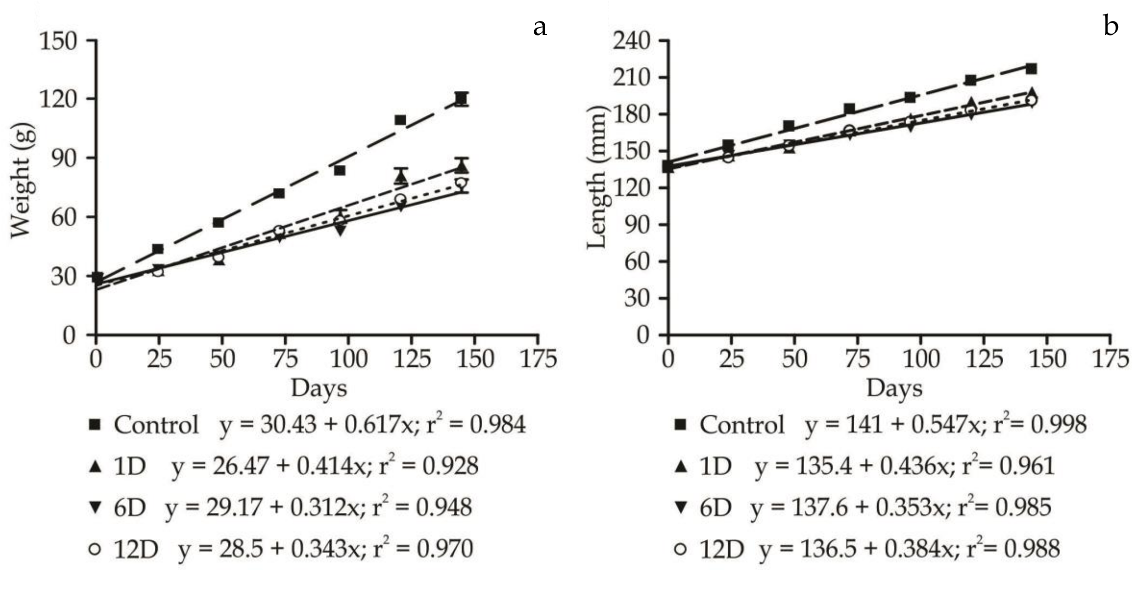

Figure 1. Relationship between weight-time (a) and total length-time (b) of juvenile *Leporinus obtusidens* subjected to four cyclic feeding regimes (days fed to apparent satiation × days without food): control (144F:0D), 1D (1F:1D), 6D (6F:6D) or 12D (12F:12D) after 144 days.

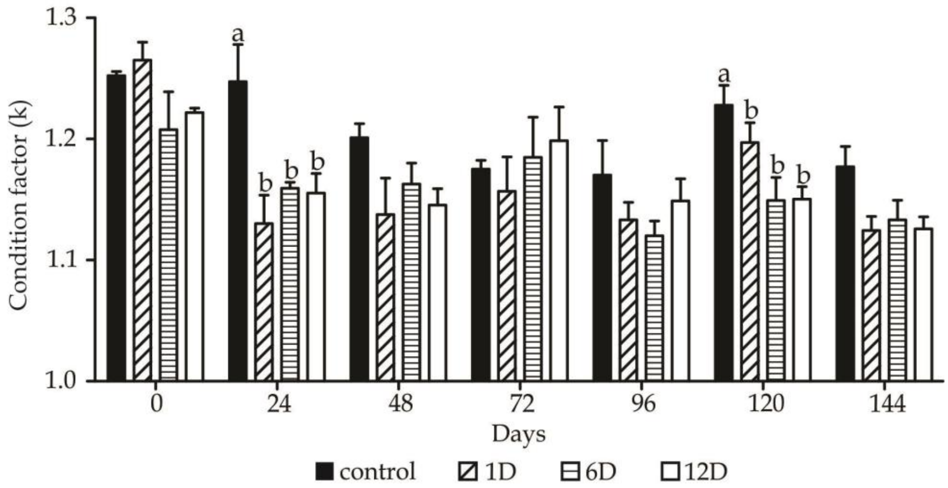

Figure 2. Condition factor (K; mean ± SD) of juvenile *Leporinus obtusidens* subjected to four cyclic feeding regimes (days fed to apparent satiation x days without food): control (144F:0D), 1D (1F:1D), 6D (6F:6D) or 12D (12F:12D) after 144 days. Different letters on the same day indicate statistical differences (P<0.05). Bars without letters indicate days with no statistical significance between feeding regimes (P>0.05).

Considering the daily food intake over the experimental period (Figure 3), differences were observed between treatments, and from day 48 in 1D and 6D, the recorded feed consumption was equal to or higher than that in control, even in a shorter feeding time.

At the end of the study, feed conversion, protein retention coefficient, intestine relative length, hepatosomatic index and visceral fat index were similar for all treatments (P>0.05).

The body composition of juvenile piava is presented in Table 2. Differences were only recorded for water content, which was higher in control treatment, whereas no difference was found for other variables.

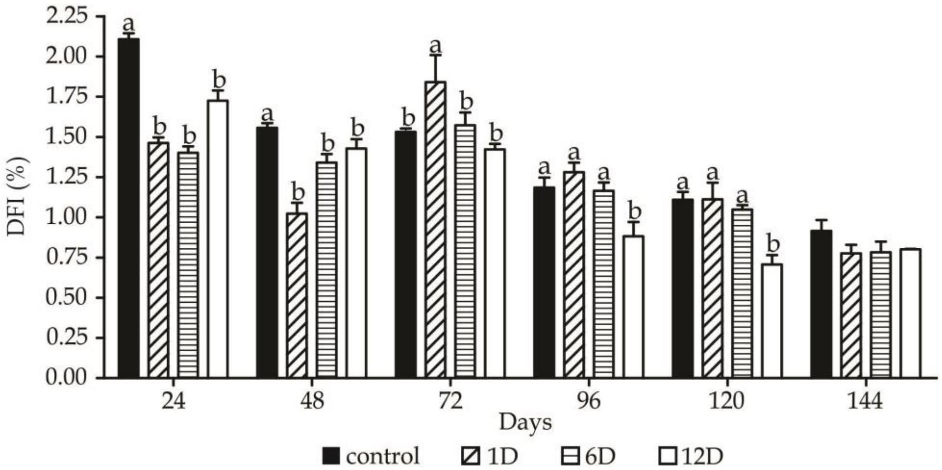

Figure 3. Daily food intake (DFI; mean ± SD) of diet by juvenile *Leporinus obtusidens* subjected to four cyclic feeding regimes (days fed to apparent satiation x days without food): control (144F:0D), 1D (1F:1D), 6D (6F:6D) or 12D (12F:12D) after 144 days. Different letters on the same day indicate statistical differences (P<0.05). Bars without letters indicate days with no statistical significance between feeding regimes (P>0.05).

Table 2. Body composition (mean ± SD) of juvenile *Leporinus obtusidens* subjected to four cyclic feeding regimes (days fed to apparent satiation × days without food): control (144F:0D), 1D (1F:1D), 6D (6F:6D) or 12D (12F:12D) for 144 days. Different letters in each column indicate significant differences (P<0.05).

Treatment	Humidity **	Crude protein *	Ether extract *	Ash*
Control	32.3 ± 0.59	20. 1 ± 1.82	9.8 ± 1.01	3.5 ± 0.16
1D	29.9 ± 1.51^{b}	20.6 ± 0.79^{a}	8.5 ± 0.69^{a}	3.9 ± 0.92^{a}
6D	29.7 ± 0.38^{b}	21.1 ± 0.42^{a}	8.2 ± 0.51^{a}	3.8 ± 0.04^{a}
12D	30.6 ± 0.62^{b}	21.2 ± 1.55^{a}	8.2 ± 0.66^{a}	3.6 ± 0.27^{a}

*** % of dry matter; * % of wet matter*

DISCUSSION

A continuous daily food supply promoted the highest weight-gain in juvenile *L. obtusidens*, but feeding regimes 1D, 6D and 12D, which alternated food deprivation and refeeding, promoted a partial recovery of growth, i.e., partial compensatory growth.

The 6D and 12D treatments showed a similar growth trend, indicating that longer periods of deprivation might favor compensatory growth, since hyperphagic responses and compensatory growth depend on the intensity and duration of food deprivation (JOBLING *et al*., 1993). This type of compensation is the most common response recorded in fish (ALI *et al*., 2003; JOBLING and JOHANSEN, 1999), although full compensation has already been reported for some species (DOBSON and HOLMES, 1984; QUINTON and BLAKE, 1990; SAETHER and JOBLING, 1999; ROHUL-AMIN *et al*., 2012).

Similarly, a lower growth response was reported for other fish species, such as channel catfish, *Ictalurus punctatus*, when fed once weekly (BOSWORTH and WOLTERS, 2005). For *Pangasianodon hypophthalmus* subjected to alternate feed cycles, optimal growth was recorded in control treatment with daily feeding, but fish submitted to a regime that alternated one day of feeding with one day of deprivation performed similarly (ROHUL-AMIN *et al*. 2012), indicating that this species readily recovers energy losses. For *Sparus aurata*, TUFAN *et al*. (2006) used a feeding regime where animals were fed to satiety for two, three or four days, followed by one day of food deprivation, for five weeks. At the end of the study, final weight and weight gain was similar for fish fed daily and for fish fed for two days followed by one day of deprivation, thus indicating the presence of a compensatory response to short periods of food deprivation and refeeding.

In short periods of deprivation (1D), *L. obtusidens* was able to replenish energy reserves and grow, but without achieving complete compensatory growth and therefore even short periods of deprivation result in significant damage to the cultivation. Over longer deprivation periods, fish also replenished their reserves, but grew slightly. In this sense, for *L. obtusidens* to reach full compensation, more refeeding days than deprivation days in short or long term cyclical periods would be necessary.

On days 24 and 120, fish in 1D, 6D and 12D treatments showed a reduction in condition factor, indicating the use of body reserves, which is usually related to changes in the quality or in this case, to the amount of food (WOOTON, 1990).

Periodic food deprivation had no effect on feed conversion, however, the daily food intake varied greatly between treatments and between different periods of cultivation. From day 72, however, intakes became similar, since fish subjected to starvation adapted to the feed conditions, but fish in 12D treatment showed a reduction in food intake. Fish in 1D regime had periods of hyperphagia and thereafter, the animals grew at a faster rate than those in 6D or 12D regimes.

According to the lipostatic model proposed by JOBLING and JOHANSEN, (1999), adipose tissue has a regulatory role in the control of appetite. Reduction in the proportion of fat relative to lean body mass during fasting induces hyperphagia, and hence, compensatory growth during refeeding. However, this compensatory growth ended when fat reserves were reestablished.

During food deprivation, animals mobilize endogenous energy reserves to maintain vital processes (COOK *et al*., 2000), which results in the loss of body weight (WEATHERLEY and GILL, 1987). During refeeding, nutrients are allocated for restoration of energy reserves, slowing growth.

CONCLUSIONS

The productive performance and the final body composition of *L. obtusidens* can be adjusted to lipostatic model.

The absence of differences in lipid levels and in visceral fat index between *L. obtusidens* from different treatments indicates that energy reserves were reestablished; however, the consumption was not sufficient to reestablish growth rates at the level shown in control treatment. Therefore *L. obtusidens* did not present compensatory growth in the condition of this study.

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