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Recovery growth of *Cherax quadricarinatus* juveniles fed on two high-protein diets: Effect of daily feeding following a cyclic feeding period on growth, biochemical composition and activity of digestive enzymes

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ABSTRACT

Recovery growth of *C. quadricarinatus* juveniles was evaluated during a daily feeding period that followed a cyclic feeding period, by the analysis of the biochemical composition and structure of the hepatopancreas, and the activity of digestive enzymes. Two different diets were evaluated: diet A (49% crude protein) and diet B (38% crude protein), and juveniles were subjected to one of the following feeding regimes for each diet: DF, under which they were daily fed throughout the experimental period (120 days); and 4F/4D, under which they were fed for 4 days followed by 4 days of food deprivation in repeated cycles from day 1 to day 45, and daily fed from day 45 to day 120. Juveniles under the 4F/4D regime showed compensatory growth and reached the same body mass of control juveniles (*i.e.* complete catch-up growth) at the end of the experiment. This physiological response was not affected by the two high-protein diets tested, and it may be at least partly explained by an improved food conversion ratio, a similar ability to digest and absorb nutrients and an increased efficiency in protein digestion with respect to control juveniles. The 4F/4D regime had no negative effects on the nutritional state and health of red claw crayfish, which confirms the high tolerance of the species to food deprivation. The present results are important from an economical point of view since they show that it is possible to significantly reduce the amount of food offered in culture systems, and consequently reduce production costs, without affecting juvenile growth.

1. Introduction

Crustacean production has increased yearly in quantity and variety, and it accounts nowadays for 21.7% of total aquaculture volumes in America, with the growing culture of freshwater crustaceans eroding the dominance of finfish in production (FAO, 2012). In relatively recent times, the culture of the red claw crayfish *Cherax quadricarinatus*, which is native to freshwater bodies from Australia and Papua New Guinea, has begun to develop. This crayfish has several physical, biological and commercial attributes that make it suitable for aquaculture, including rapid growth, non-aggressive and non-burrowing behavior, and tolerance to high stocking densities. It is also able to modulate some characteristics of digestive physiology in response to changes in nutritional requirements, food availability and dietary profile. The development of this crayfish is direct (*i.e.* the adult morphology is achieved without progression through a morphologically distinct, free-living larval phase), which greatly simplifies juvenile production. The species is cultured in extensive and semi-intensive systems, with straightforward production technology (Saoud et al., 2013). However, intensive juvenile production is still hindered in hatchery–nursery systems by the lack of efficient and reliable hatchery protocols and the formulation of few diets meeting the specific requirements of the redclaw crayfish (Saoud and Ghanawi, 2012; Saoud et al., 2012). Diets containing a mixture of plant and animal protein sources usually result in better growth since they generally meet or exceed the nutritional requirements. In particular, *C. quadricarinatus* juveniles grow rapidly and high-protein diets (containing at least 35% crude protein) are needed to obtain adequate growth in closed recirculating systems (Saoud et al., 2012).

Many studies have focused on the growth performance of commercially important aquatic organisms under different feeding-starvation regimes in order to improve the productivity of aquaculture systems. Of particular interest is the recovery growth shown by some species

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after a food deprivation or restriction period, which may be the result of compensatory growth (*i.e.* abnormally rapid growth) combined with complete catch-up growth (*i.e.* convergence of growth trajectories of animals that have different growth histories), as stated by Jobling (2010). Both physiological responses are advantageous since they may allow producers to reduce the amount of food provided (and consequently feed costs), improve water quality by minimizing food waste, increase food utilization and growth efficiency, and save personnel time (Ali et al., 2003; Cho and Heo, 2011; Sevgili et al., 2012; Turano et al., 2008; Yengkokpam et al., in press).

Recovery growth can be influenced by several factors, such as size or age, feeding regimes and nutrient levels in the diet (Gaylord and Gatlin, 2001; Oh et al., 2008; Tian and Qin, 2003; Xiao et al., 2013). Stumpf et al. (2010, 2011, 2012a, 2012b) evaluated the growth performance of *C. quadricarinatus* juveniles of <360 mg (reared individually) and 1 g (reared in groups) after different cyclic feeding periods, and showed that only the former underwent compensatory growth with complete/partial catch-up growth. This response was influenced by the developmental stage, cyclic feeding protocols and duration of the cyclic feeding period. The absence of a daily feeding period following the cyclic feeding period may be a possible explanation for the inability of 1 g juveniles reared in groups to undergo compensatory growth (Stumpf et al., 2012b).

It has been suggested that compensation with complete catch-up growth is associated with hyperfagia, improved growth efficiency and replenishment of energy reserves (Ali et al., 2003; Álvarez and Nicieza, 2005). Energy reserves are produced from the catabolism of dietary compounds and stored in specialized tissues. In decapod crustaceans, the biochemical energy reserves are composed of proteins, lipids and glycogen (Anger, 2001). On this basis, the evaluation of the digestive machinery through the analysis of the main digestive enzymes may be a potential tool to determine to what extent cyclic and daily feeding periods govern nutrient utilization (Furné et al., 2008). In crustaceans, the site of temporal and cyclic retention of energy reserves, synthesis and secretion of digestive enzymes (proteases, carbohydrases, and lipases), and nutrient absorption is the hepatopancreas (Gibson and Barker, 1979). The digestion and absorptive capacity of this gland correlate with its size and cellular structure and are associated with the activity of digestive enzymes (Gao et al., 2006; Secor et al., 2000). Changes in these parameters may reflect a physiological response to different nutritional conditions (Le Moullac et al., 1997; Sánchez-Paz et al., 2007).

To our knowledge, the compensatory growth of *C. quadricarinatus* juveniles reared in groups has never been reported and no studies have evaluated the effect of cyclic feeding on the activity of digestive enzymes. This information could be used to increase yields in large-scale production of this important decapod crustacean. Based on the considerations mentioned above, the objectives of the present study were to evaluate: (1) the recovery growth of *C. quadricarinatus* juveniles (1 g) during a daily feeding period that followed a cyclic feeding period, under high-density conditions; (2) the influence of two different diets on that response; and (3) the nutritional changes associated with the cyclic feeding and daily feeding periods, by means of histological and enzymatic analyses of the hepatopancreas and the analysis of energy reserves in the hepatopancreas and abdominal muscle.

2. Materials and methods

2.1. Animals

The juveniles used in the present study were obtained under laboratory conditions, from a reproductive stock supplied by Centro Nacional de Desarrollo Acuícola (CENADAC), Corrientes, Argentina. Several ovigerous females were placed in individual glass aquaria (60 × 40 × 30 cm) containing 30 L of dechlorinated tap water (pH 7–8, hardness 70–100 mg/L as $CaCO_3$ equivalents) under continuous aeration to maintain a dissolved oxygen concentration of 5–8 mg/L. Water temperature was held constant at 27 ± 1 °C by ATMAN (China) water heaters (100 W) and the photoperiod was 14:10 h (light:dark), according to Jones (1997). Females were fed daily *ad libitum* with *Elodea* sp. and commercial balanced food for tropical fish Tetracolor, TETRA®, with the following composition: protein 49.5%, lipid 4.6%, fiber 2.0%, moisture 6.4%, phosphorus 1.5% and ascorbic acid 0.1%. This diet is adequate for growth and reproduction of the species under laboratory conditions (Sánchez De Bock and López Greco, 2010; Stumpf et al., 2010). After reaching the free-living stage III (Levi et al., 1999), juveniles were separated from their mothers and maintained in glass aquaria (60 × 40 × 30 cm) under the same conditions of water quality, temperature, photoperiod and feeding described above, until reaching an approximate mass of 1 g.

2.2. Experimental diets and feeding regimes

The experiment was performed in order to test the effect of two different diets on the compensatory response and catch-up growth of juveniles: *Diet A* (*crude protein 49%*), which was the commercial balanced food used for ovigerous females; and *Diet B* (*crude protein 38%*), which was formulated for *C. quadricarinatus* by Gutiérrez and Rodríguez (2010) and used for juvenile rearing under laboratory conditions by Sacristán et al. (2010, 2011). The use of two diets with high protein content responds to the fact that *C. quadricarinatus* juveniles show high protein requirements during the first stages of development as a result of their high dietary nutrient digestibility (Campaña, 2001). The digestibility of diet A has been demonstrated to be higher than that of diet B (Sacristán et al., 2010, 2011). The nutritional composition of both diets is described in Table 1. Juveniles were acclimated to the experimental diet for one week prior to the onset of the experiment.

The feeding regimes were: *Control* (*DF*), under which juveniles were daily fed throughout the experimental period (120 days); and *Cyclic Feeding* (*4F/4D*), under which juveniles were fed for 4 days followed by 4 days of food deprivation in repeated cycles during the first 45 days of the experimental period (cyclic feeding period), and daily fed from day 45 to day 120 (daily feeding period). These feeding regimes were selected based on previous results (Stumpf et al., 2012a, 2012b).

2.3. Experimental procedure

One hundred and twenty juveniles weighing 0.91 ± 0.02 g were randomly selected and assigned to one of the following treatments: DF–Diet A, 4F/4D–Diet A, DF–diet B and 4F/4D–diet B. Each treatment had six replicates. Juveniles were maintained in glass aquaria (60 × 40 × 30 cm) filled with 40 L of dechlorinated tap water. Each aquarium was a replicate and had 5 juveniles (21 crayfish/m^2). They were fed at 4% of body mass during the first 75 days of the

Table 1
Proximate composition of the experimental diets, according to Sacristán et al. (2010, 2011).

Nutrients	Diet A [1]	Diet B [2]
Crude protein (%)	49.51 ± 0.09	37.98 ± 0.94
Total lipids (%)	4.60 ± 0.02	6.05 ± 0.08
Ash (%)	8.76 ± 0.00	16.05 ± 0.11
Moisture (%)	6.45 ± 0.04	4.03 ± 0.03

[1] Fish meal, dehulled soybean meal, wheat germ meal, wheat flour, corn gluten, feeding oat meal, potato protein, shrimp meal, dried yeast, wheat gluten, algae meal, soybean oil, monobasic calcium phosphate, beta-carotene, annato extract, red 3. Mineral premix ($ZnSO_4$; $MnSO_4$; $FeSO_4$; $Co(CH_3CO_2)_2$). Vitamin premix (A (retinol); D; B1; B12; B; B6; D3; lysine; lecithin; C (ascorbic acid); L-ascorbyl-2-polyphosphate (stabilized vit. C); E (alpha tocopheryl acetate); folic acid; biotin; B12; B5 (pantothenic acid); $C_5H_{14}ClNO$).
[2] Fish meal, soybean meal, pre-jellified starch, soybean oil, bentonite, astaxanthin mineral premix ($ZnSO_4$; $MgSO_4$; $MnSO_4$; $CoSO_4$; $CuSO_4$; KI), vitamin premix (A (retinol); D; E (alpha tocopheryl acetate); K; C (ascorbic acid); B1 (thiamin); B (riboflavin); Vitamin B6 (piridoxin); B12; biotin; B5 (pantothenic acid); folic acid; niacin; choline; inositol).

experimental period, and at 2% of body mass on subsequent days. To reduce the effect of this high density on juvenile growth and survival 10 PVC tubes (2 cm in diameter and 10 cm long) and 3 pieces (60 × 34 cm) of synthetic net of 1-cm pore size were provided *per* aquarium as shelters (Calvo et al., 2013).

The experiment was performed under the same conditions of photoperiod, temperature and water aeration as described for ovigerous females. In all cases, 50% of the aquarium water was replaced every 4 days from day 1 to day 45 to ensure the removal of food waste prior to food deprivation for the 4F/4D regime. Water was replaced every 7 days from day 45 onward.

2.4. Sample collection and analysis

Juveniles were weighed every 2 weeks. Three of the six replicates of each treatment were randomly selected at day 45 (end of the cyclic feeding period) and all the juveniles from these replicates were sacrificed after being cold-anesthetized at −20 °C for 15 min. The hepatopancreas and pleon were rapidly dissected and weighed on an analytical balance (precision 0.1 mg). Pieces of two hepatopancreas (corresponding to two juveniles) *per* replicate (n = 6 *per* treatment) were fixed in Bouin's solution for histological analyses. The samples were then dehydrated in alcohol series and embedded in paraffin. Sections (6 μm thick) were stained with hematoxylin–eosin (López Greco et al., 2007) and characterized based on recent descriptions of the hepatopancreas structure for the species (Calvo et al., 2011).

Pieces of three/five hepatopancreas *per* replicate (n = 9/15 *per* treatment) were oven-dried at 60 °C to a constant mass to determine the moisture content and hepatopancreas dry mass. Three/five abdominal muscles (n = 9/15 *per* treatment) and the remaining hepatopancreas were stored at −70 °C for biochemical and enzymatic analysis.

Total proteins, total lipids and glycogen were determined spectrophotometrically in homogenates of tissues from 3/5 juveniles *per* replicate (n = 9–15 *per* treatment) according to the methods described by Bradford (1976), Folch et al. (1957) (modified by Frings and Dunn, 1970), and Van Handel (1965) (modified by Geary et al., 1981), respectively.

For protein determination, pieces of hepatopancreas and abdominal muscle weighing approximately 150 mg were homogenized in 600 μL of 50 mM Tris–HCl buffer, pH 7.5, and centrifuged at 10,000 ×*g* for 30 min in a cooling centrifuge (4 °C). Total proteins were estimated in the supernatant by the Coomassie blue dye method, with bovine serum albumin as a standard. Absorbance was read at 595 nm. For lipid determination, pieces of hepatopancreas and abdominal muscle weighing approximately 60–80 mg were homogenized in 3.6–2.4 mL of a mixture of chloroform and methanol (2:1, v/v), then mixed and centrifuged with 0.9% NaCl to separate the lipid fraction. Total lipids were quantified by the sulfophosphovanillin method, with olive oil dilute with absolute ethanol as standard. Absorbance was read at 530 nm. For glycogen determination, pieces of hepatopancreas and abdominal muscle weighing approximately 60–80 mg were boiled with KOH 30% for 1 h. Following separation, glycogen was precipitated with the addition of saturated Na_2SO_4 and absolute ethanol, and centrifugation at 3500 ×*g* for 10 min. Then, it was dissolved by the addition of 300 μL of distilled water, and glycogen levels were determined as glucose equivalent using a glycemia commercial kit (Wiener-Lab AA), after acidic hydrolysis with HCl 4N and neutralization with Na_2CO_3 2 M. Rabbit liver (Fluka) was used as standard and absorbance was read at 505 nm.

The activity of the hepatopancreas digestive enzymes (proteases, lipase and amylase) was determined in homogenates of hepatopancreas from 3/5 juveniles *per* replicate (n = 9–15 *per* treatment), using the methods described by García-Carreño (1992), Versaw et al. (1989) and Vega-Villasante et al. (1993), respectively.

Protease activity was assayed using 0.5% azocasein as the substrate in 50 mM Tris–HCl buffer, pH 7.5. Absorbance was read at 440 nm. Lipase activity was determined in a mixture of 100 μL of sodium taurocholate (100 mM), 920 μL of 50 mM Tris–HCl buffer (pH 8) and 10 μL of enzyme extract. Following the addition of 10 μL of β-naphthyl caprylate substrate [100 mM in dimethyl sulfoxide (DMSO)], the mixture was incubated at room temperature (25 °C ± 1) for 30 min. Then, 10 μL of Fast Blue BB (100 mM in DMSO) was added and the mixture was incubated at the same temperature for 5 min. The reaction was stopped with 100 μL TCA (12%), and clarified with 1.35 mL of ethyl acetate:ethanol (1:1 $V * V^{-1}$). Absorbance was recorded at 540 nm. Amylase activity was assayed in a mixture of 500 μL of 50 mM Tris–HCl (pH 7.5), 5 μL of enzyme extract, and 500 μL of starch solution (1% in 50 mM Tris–HCl, pH 7.5). The mixture was incubated at room temperature (25 °C ± 1) for 10 min. Enzyme activity was determined by measuring the production of reducing sugars resulting from starch hydrolysis, as follows: immediately after incubation, 200 μL of sodium carbonate (2 N) and 1.5 mL of DNS reagent were added to the mixture, which was boiled for 15 min. Volume was adjusted to 7.3 mL with distilled water, and the absorbance was read at 550 nm.

The procedures described above were also performed at day 120 (end of the experiment) with the remaining three replicates.

2.5. Data calculation

All variables were calculated on a wet mass basis for both experiments, except the hepatosomatic index, which was also calculated on a dry mass basis. The formulae used to calculate the different indices were as follows: Survival (S, % = [final number of crayfish / initial number of crayfish] * 100); Specific growth rate (SGR, % / day = [ln final body mass − ln initial body mass / days] * 100); Apparent feed conversion ratio (AFCR = [total food provided / total mass gain]); Apparent protein efficiency ratio (APER = mass gain / protein provided); Apparent lipid efficiency ratio (ALER = mass gain / lipid provided); Hepatosomatic index (HSI, % = [hepatopancreas mass / final body mass] * 100); and Relative pleon mass (RPM, % = [pleon mass / final body mass] * 100).

2.6. Statistical analysis

All values are expressed as mean ± standard deviation. Data were tested for normality and homogeneity of variance using the Shapiro–Wilk test and Levene's F-test, respectively. A two-way ANOVA was used to evaluate the effect of the diet (fixed factor with two levels: diet A and diet B), and the feeding regime (fixed factor with two levels: control-DF and cyclic feeding-4F/4D) on the studied variables. The LSD test was applied when the interaction was significant. Differences were considered significant at $P < 0.05$. Each treatment had six replicates. All statistical analyses were performed using STATISTICA version 8.0.

3. Results

3.1. Survival, amount of food supplied, food utilization and growth

Juvenile survival at day 120 was similar between feeding regimes and diets ($P > 0.05$) with a mean value of 80% for each treatment. The total amount of food offered to the juveniles under the 4F/4D regime was 36% (diet A) and 34% (diet B) lower ($P < 0.05$) than that offered to the juveniles under the DF regime during the cyclic feeding and daily feeding periods (Table 2).

At day 45 (end of the cyclic feeding period), the body mass was 48% (diet A) and 37% (diet B) lower ($P < 0.05$) in juveniles under the 4F/4D regime than in control juveniles (Fig. 1). The latter had a higher body mass when fed with diet A, while juveniles under the 4F/4D regime had a similar body mass regardless of diet. From day 45 onward the differences in body mass drastically decreased between feeding regimes, with values being 12% (diet A) lower and 18% (diet B) higher in 4F/4D

Table 2
Production variables and growth performance of *C. quadricarinatus* juveniles under two different feeding regimes and fed on two different diets.

	Diet A		Diet B	
	DF	4F/4D	DF	4F/4D
Total food (g)				
Days 1–45	16.20 ± 0.90 A^x	6.74 ± 0.47 B^x	14.33 ± 2.02 A^y	5.97 ± 0.54 B^y
Days 45–120	86.11 ± 12.42 A	58.54 ± 2.00 B	70.79 ± 4.57 A	50.73 ± 5.92 B
Days 1–120	102.46 ± 13.37	65.46 ± 1.48	86.70 ± 4.90	57.08 ± 6.12
Body mass (g)				
Day 1	0.91 ± 0.01	0.92 ± 0.01	0.91 ± 0.01	0.91 ± 0.01
Day 45	4.71 ± 0.15 a	2.15 ± 0.09 c	3.76 ± 0.21 b	2.39 ± 0.12 c
Day 120	12.53 ± 1.34	11.00 ± 1.43	13.63 ± 1.90	16.11 ± 3.51
Specific growth rate (%/day)				
Days 1–45	3.64 ± 0.06 a	2.19 ± 0.08 b	3.13 ± 0.12 c	2.13 ± 0.10 b
Days 45–120	1.28 ± 0.13 B	1.86 ± 0.23 A	1.55 ± 0.17 B	2.44 ± 0.22 A
Days 1–120	2.14 ± 0.08	2.03 ± 0.11	2.19 ± 0.12	2.32 ± 0.16
Apparent food conversion ratio				
Days 1–45	1.07 ± 0.06 B^x	1.15 ± 0.06 A^x	0.88 ± 0.06 B^y	1.09 ± 0.03 A^y
Days 45–120	0.50 ± 0.03 B	0.70 ± 0.04 A	0.45 ± 0.09 B	0.79 ± 0.06 A
Days 1–120	0.52 ± 0.01	0.66 ± 0.06	0.49 ± 0.09	0.79 ± 0.07
Apparent protein efficiency ratio				
Days 1–45	0.45 ± 0.04	0.46 ± 0.05	0.55 ± 0.08	0.44 ± 0.12
Days 45–120	0.19 ± 0.05 B^y	0.29 ± 0.08 A^y	0.36 ± 0.12 B^x	0.72 ± 0.31 A^x
Apparent lipid efficiency ratio				
Days 1–45	5.10 ± 0.44 ^{x}	4.95 ± 0.54 ^{x}	3.46 ± 0.52 ^{y}	2.76 ± 0.74 ^{y}
Days 45–120	2.01 ± 0.05 B	3.12 ± 0.9 A	2.26 ± 0.76 B	4.53 ± 1.96 A

Feeding regimes: DF (juveniles fed daily throughout the experimental period); 4F/4D (juveniles fed for 4 days followed by 4 days of food deprivation in repeated cycles during the first 45 days of the experimental period, and fed daily from day 45 to day 120). Values are means ± standard deviation of six (days 1–45) or three (days 45–120) replicates *per* treatment. Different lowercase letters in the same row indicate significant ($P < 0.05$) interaction between diets and feeding regimes (*i.e.* between DF and 4F/4D for each diet and between diets A and B for each feeding regime); different capital letters in the same row indicate significant differences ($P < 0.05$) between feeding regimes (DF and 4F/4D); different superscripts in the same row indicate significant differences ($P < 0.05$) between diets (A and B).

than in DF at day 120 (Fig. 1). However, no statistical difference ($P > 0.05$) was found for this variable at day 120 (Table 2).

The specific growth rate showed the same pattern of variation as body mass at day 45 (Table 2). At the end of the daily feeding period, that variable was significantly higher ($P < 0.05$) in juveniles under the 4F/4D regime than in control juveniles (Table 2).

The apparent feed conversion ratio was significantly better ($P < 0.05$) for the former during the cyclic feeding and the daily feeding periods, and it was higher ($P < 0.05$) for juveniles fed with diet A than those fed with diet B, but only during the first 45 days of the experimental period (Table 2).

The apparent protein efficiency ratio was similar ($P > 0.05$) among treatments at the end of the cyclic feeding period. At the end of the daily feeding period, this variable was better ($P < 0.05$) for juveniles under the 4F/4D regime than control juveniles and for diet B than diet A (Table 2). The apparent lipid efficiency ratio was better ($P < 0.05$) for juveniles fed with diet A than those fed with diet B at day 45, and better ($P < 0.05$) for the 4F/4D regime than the DF regime at day 120 (Table 2).

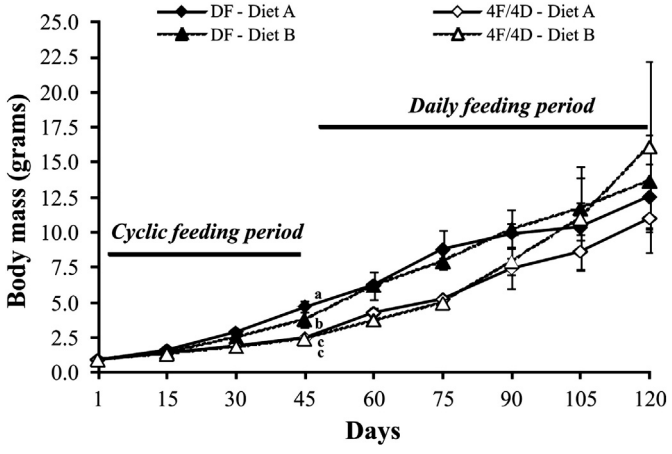

Fig. 1. Wet body mass of *Cherax quadricarinatus* juveniles over a 120-day period. Feeding regimes: DF (juveniles fed daily throughout the experimental period); 4F/4D (juveniles fed for 4 days followed by 4 days of food deprivation in repeated cycles during the first 45 days of the experimental period, and fed daily from day 45 to day 120). Values are means ± standard deviation of six (days 1–45) or three (days 45–120) replicates *per* treatment. Different lowercase letters at day 45 indicate significant ($P < 0.05$) interaction between diets and feeding regimes (*i.e.* between DF and 4F/4D for each diet and between diets A and B for each feeding regime).

Table 3
Wet and dry hepatosomatic index (HSI) and relative pleon mass (RPM) of *C. quadricarinatus* juveniles under two different feeding regimes and fed on two different diets.

	Diet A		Diet B	
	DF	4F/4D	DF	4F/4D
Hepatopancreas				
Wet HSI				
Day 45	7.5 ± 0.2 ^{y}	7.7 ± 0.2 ^{y}	8.6 ± 0.5 ^{x}	8.4 ± 0.9 ^{x}
Day 120	7.3 ± 0.3	8.0 ± 0.4	8.9 ± 0.5	8.0 ± 0.5
Dry HSI				
Day 45	2.4 ± 0.3	2.4 ± 0.4	3.2 ± 0.7	2.7 ± 0.3
Day 120	2.2 ± 0.1 c	2.5 ± 0.4 c	4.6 ± 0.6 a	3.5 ± 0.6 b
Pleon				
Wet pleon				
Day 45	32.2 ± 0.8	31.9 ± 0.7	31.9 ± 0.9	32.2 ± 1.2
Day 120	30.7 ± 0.8	32.4 ± 0.5	33.4 ± 3.0	32.8 ± 1.1

Feeding regimes: DF (juveniles fed daily throughout the experimental period); 4F/4D (juveniles fed for 4 days followed by 4 days of food deprivation in repeated cycles during the first 45 days of the experimental period and fed daily from day 45 to day 120). Values are means ± standard deviation of three replicates *per* treatment. Different lowercase letters in the same row indicate significant ($P < 0.05$) interaction between diets and feeding regimes (*i.e.* between DF and 4F/4D for each diet and between diets A and B for each feeding regime); different superscripts in the same row indicate significant differences ($P < 0.05$) between diets (A and B).

3.2. Hepatopancreas and abdominal muscle: indices

Juveniles fed with diet B had a higher ($P < 0.05$) wet hepatosomatic index (HSI) than those fed with diet A at the end of the cyclic feeding period; no statistical difference ($P > 0.05$) was detected for the dry HSI at the end of this period (Table 3). The wet HSI was similar between feeding regimes and diets at day 120 ($P > 0.05$). A significant interaction ($P < 0.05$) was detected between feeding regimes and diets for the dry HSI at day 120, with this variable being similar between feeding regimes when juveniles were fed with diet A and lower for juveniles under the 4F/4D regime than in those under the DF regime, when fed with diet B (Table 3). The dry HSI was higher ($P < 0.05$) for juveniles fed with diet B than fed with diet A. The relative pleon mass was not affected ($P > 0.05$) by diet and feeding regime (Table 3).

3.3. Histology of the hepatopancreas

The histological examination of the hepatopancreas revealed no structural differences between feeding regimes for both diets. This gland had a normal structure in all cases, based on Calvo et al. (2011).

3.4. Hepatopancreas and abdominal muscle: energy reserves

The protein content in the hepatopancreas was higher ($P < 0.05$) in juveniles fed with diet B than those fed with diet A at day 45. This variable, as well as the lipid and glycogen contents, were similar ($P > 0.05$) between feeding regimes and diets at day 120.

The lipid content in the abdominal muscle was higher ($P < 0.05$) in juveniles fed with diet A than in those fed with diet B at days 45 and 120. At day 45, the glycogen content in the abdominal muscle was higher ($P < 0.05$) in juveniles fed with diet B than in those fed with diet A. This variable was similar ($P > 0.05$) between feeding regimes and diets at day 120. The same was observed for the protein content throughout the experiment (Table 4).

Table 4
Energy reserves in the hepatopancreas and abdominal muscle of *C. quadricarinatus* juveniles under two different feeding regimes and fed on two different diets.

	Diet A		Diet B	
	DF	4F/4D	DF	4F/4D
Wet hepatopancreas				
Total protein (mg/g)				
Day 45	35.9 ± 2.2 ^{y}	31.3 ± 5.3 ^{y}	44.8 ± 1.8 ^{x}	45.9 ± 6.8 ^{x}
Day 120	41.7 ± 16.4	42.8 ± 16.4	44.0 ± 10.1	33.5 ± 4.1
Total lipids (mg/g)				
Day 45	83.8 ± 41.9	79.7 ± 8.2	128.0 ± 58.0	175.2 ± 106.8
Day 120	214.9 ± 11.4	206.2 ± 98.0	310.2 ± 82.5	222.6 ± 28.9
Glycogen (mg/g)				
Day 45	2.1 ± 0.6	1.5 ± 0.7	2.4 ± 1.1	2.7 ± 0.9
Day 120	2.2 ± 0.3	2.8 ± 1.9	1.1 ± 1.0	0.9 ± 0.5
Wet abdominal muscle				
Total protein (mg/g)				
Day 45	58.5 ± 11.3	62.1 ± 2.1	41.7 ± 13.8	60.9 ± 11.4
Day 120	67.4 ± 17.1	81.1 ± 10.0	70.5 ± 7.5	64.1 ± 0.1
Total lipids (mg/g)				
Day 45	3.9 ± 0.6 ^{x}	4.3 ± 1.6 ^{x}	1.1 ± 0.7 ^{y}	1.6 ± 0.5 ^{y}
Day 120	5.8 ± 1.7 ^{x}	4.9 ± 0.6 ^{x}	2.7 ± 0.9 ^{y}	3.1 ± 0.2 ^{y}
Glycogen (mg/g)				
Day 45	1.2 ± 0.4 ^{y}	2.2 ± 0.7 ^{y}	17.2 ± 7.9 ^{x}	10.8 ± 3.2 ^{x}
Day 120	6.6 ± 3.3	4.5 ± 1.3	9.7 ± 7.2	6.0 ± 2.4

Feeding regimes: DF (juveniles fed daily throughout the experimental period); 4F/4D (juveniles fed for 4 days followed by 4 days of food deprivation in repeated cycles during the first 45 days of the experimental period and fed daily from day 45 to day 120). Values are means ± standard deviation of three replicates *per* treatment. Different superscripts in the same row indicate significant differences ($P < 0.05$) between diets (A and B).

3.5. Hepatopancreas: activity of the digestive enzymes

The protease activity was similar ($P > 0.05$) between feeding regimes and diets at day 45, but it was higher ($P < 0.05$) in juveniles under the 4F/4D regime with respect to the control juveniles for both diets at day 120. The amylase activity was higher ($P < 0.05$) in juveniles under the DF regime than in those under the 4F/4D regime for both diets, and it was higher ($P < 0.05$) in juveniles fed with diet A than in those fed with diet B at day 45. At day 120, juveniles fed with diet B showed a higher activity of this enzyme than those fed with diet A. No statistical differences ($P > 0.05$) were found in the lipase activity between feeding regimes and diets at days 45 and 120 (Table 5).

4. Discussion

The present results show for the first time the ability of *C. quadricarinatus* juveniles to undergo compensatory growth and reach the same body mass of control juveniles (*i.e.* complete catch-up growth) after a cyclic feeding period when reared in groups. The restoration of feeding and the duration of the daily feeding period were important factors for recovery growth. This physiological response was not influenced by diet composition (protein content: 49 and 38% in diet A and B, respectively) and nutrient bioavailability (higher in diet A than diet B), and is consistent with the response previously observed in juveniles of the species reared in individual containers (Stumpf et al., 2010, 2011).

Some physiological mechanisms such as hyperphagia and improvement in food conversion ratio have been proposed to be associated with recovery growth (Bélanger et al., 2002; Jiwyam, 2010; Sevgili et al., 2012; Xiao et al., 2013; Yengkokpam et al., in press). In the present study, the recovery growth shown by juveniles when normal feeding conditions were restored may be at least partially attributed to an improvement in the apparent food conversion ratio (consistently observed throughout the experiment), which may be due, in turn, to decreased energetic demands, improved retention rates or the increased activity of digestive enzymes (Anger, 2001; Furné et al., 2008; Gaylord and Gatlin, 2001). Although not measured, it is probable that the food consumption of juveniles under the 4F/4D regime was higher during the first 15 days of the daily feeding period, since the increase in specific growth rate was more pronounced during that period (3.21%/day for diet A and 2.85%/day for diet B) than in the last 15 days of the cyclic feeding period (1.51%/day for diet A and 1.84%/day for diet B). Future

Table 5
Activity of the digestive enzymes in the hepatopancreas of *C. quadricarinatus* juveniles under two different feeding regimes and fed on two different diets.

	Diet A		Diet B	
	DF	4F/4D	DF	4F/4D
Wet hepatopancreas				
Protease activity (U/mg protein ∗ min)				
Day 45	0.6 ± 0.2	0.6 ± 0.2	0.5 ± 0.1	0.3 ± 0.2
Day 120	0.5 ± 0.2 B	0.8 ± 0.1 A	0.4 ± 0.1 B	0.5 ± 0.1 A
Lipase activity (U/mg protein ∗ min)				
Day 45	147.3 ± 12.4	174.6 ± 34.0	145.8 ± 80.3	209.6 ± 44.7
Day 120	115.4 ± 7.9	231.5 ± 73.5	170.9 ± 93.6	179.0 ± 52.8
Amylase activity (U/mg protein ∗ min)				
Day 45	11.9 ± 2.4 A^{x}	8.0 ± 2.0 B^{x}	6.2 ± 1.4 A^{y}	5.8 ± 1.2 B^{y}
Day 120	3.3 ± 0.7 ^{y}	3.5 ± 0.6 ^{y}	4.0 ± 1.2 ^{x}	5.1 ± 1.5 ^{x}

Feeding regimes: DF (juveniles fed daily throughout the experimental period); 4F/4D (juveniles fed for 4 days followed by 4 days of food deprivation in repeated cycles during the first 45 days of the experimental period and fed daily from day 45 to day 120). Values are means ± standard deviation of three replicates *per* treatment. Different lowercase letters in the same row indicate significant ($P < 0.05$) interaction between diets and feeding regimes (*i.e.* between DF and 4F/4D for each diet and between diets A and B for each feeding regime); different capital letters in the same row indicate significant differences ($P < 0.05$) between feeding regimes (DF and 4F/4D); different superscripts in the same row indicate significant differences ($P < 0.05$) between diets (A and B).

studies evaluating hyperphagia during daily feeding periods and its relationship with the food conversion ratio and specific growth rate are necessary to determine the mechanisms underlying compensatory growth with complete catch-up growth. Interestingly, the specific growth rate and food conversion ratio of juveniles under the 4F/4D regime were still higher than those of control juveniles when the experiment was over, suggesting that the growth of the former may overcome that of the latter if the daily feeding period was longer. The metabolic rate can decrease during food restriction due to a metabolic stress condition. This metabolism adjustment may extend beyond the initial days of feeding recommencement before reaching normal levels and this may increase the chances of compensatory growth (Ali and Jauncey, 2004; Ali et al., 2003). The better values of specific growth rate, food conversion ratio, protein efficiency ratio and lipid efficiency ratio observed in the present study may be due to this low metabolic expenditure.

In the present study, no mobilization of proteins, lipids and glycogen was detected at the end of the cyclic feeding period for both diets; this was also reflected by the fact that the relative pleon mass and hepatosomatic index were similar between feeding regimes for each diet. These results are in accordance with those previously obtained by Stumpf et al. (2012b), but disagree with results of other studies showing a change in the hepatopancreas indices (wet and dry) of *C. quadricarinatus* and *C. destructor* when exposed to starvation (Calvo et al., 2013; Jones and Obst, 2000). Based on the foregoing findings, it seems that body mass may be affected before any change in the biochemical composition of the main tissues becomes apparent when juveniles are exposed to cyclic changes in food availability, as previously reported by Zhu et al. (2004) for the gibel carp, *Carassius auratus gibelio*, and Chinese longsnout catfish, *Leiocassis longirostris*. It also seems that the energy needed for basal metabolism and survival during a cyclic feeding period may come from the catabolism of reserves stored in tissues other than the hepatopancreas and abdominal muscle, such as the carcass (heart, gills, *etc.*). In this sense, Powell and Watts (2010) observed a high mobilization of proteins and lipids from the carcass of the crayfishes *Procambarus clarkii* and *Procambarus zonangulus* when exposed to starvation for 5 months. In addition, crustaceans store glycogen in specialized cells of the hemolymph (*i.e.* hemocytes), which allow a more effective glucose distribution under stressful conditions than that expected for a central glycogen deposit (Rosseti, 2011).

On the other hand, at the end of the daily feeding period the dry hepatosomatic index was lower in juveniles under the 4F/4D regime than in control juveniles for diet B, but the energy reserve levels were similar between feeding regimes. According to what was observed by Hervant et al. (1999) and Van Dijk et al. (2005), a rapid and efficient storage of energy, which may be later used to synthesize new body tissues, may occur during the initial phase of a feeding period following food deprivation. For instance, glycogen content has been reported to significantly increase at the onset of feeding restoration, and decrease toward control values thereafter (Hervant and Renault, 2002; Sánchez-Paz et al., 2007). On the contrary, some studies showed that the compensatory growth of fishes was not accompanied by changes in tissue biochemical composition during the re-feeding period (Gaylord and Gatlin, 2001; Nicieza and Metcalfe, 1997; Quinton and Blake, 1990). Based on these considerations, it may be interesting to analyze in future studies the energy reserve levels in the initial phase of the daily feeding period to determine whether this parameter changes during that period.

The present results on energy reserve utilization, hepatosomatic indices and survival suggest that the nutritional state of juveniles was not affected by the cyclic feeding regime, as also demonstrated by the normal structure of their hepatopancreas. In addition, the similar activity of proteases and lipases of juveniles under both feeding regimes at day 45 may indicate that cyclically fed juveniles were as efficient in digesting proteins and lipids as daily fed juveniles. Similar results were reported for the southern catfish *Silurus meridionalis* under food deprivation conditions (Zeng et al., 2012). These findings suggest that food restriction may be compensated by a better food conversion ratio (*i.e.* better nutrient assimilation) and the maintenance of digestive enzyme activities, as previously proposed by Anger (2001). This author also stated that the energy obtained by crustaceans from food can exceed the metabolic losses due to food deprivation and consequently allows for their growth. The delayed but positive growth of cyclically fed juveniles is in accordance with that statement.

On the other hand, a higher protease activity was observed in juveniles under the 4F/4D regime, at the end of the daily feeding period, which reflects an increased ability to digest proteins from the diet. This may result in tissue synthesis and ultimately in recovery growth. Similar findings have been previously reported for the Atlantic cod *Gadus morhua* (Jobling et al., 1995), juvenile roach *Rutilus rutilus caspicus* (Abolfathi et al., 2012) and *Labeo rohita* fingerlings (Yengkokpam et al., 2013, in press).

In conclusion, *C. quadricarinatus* 1-g juveniles maintained at a density of 21 animals/m^2 showed recovery growth at the end of a 75-day period of daily feeding that followed a 45-day period of cyclic feeding. This physiological response did not seem to be affected by diet, and it may be partly explained by an improvement in the food conversion ratio and protein efficiency ratio, and an increase in the activity of proteases, during the recovery period. The 4F/4D regime evaluated in the present study had no negative effects on the nutritional state and health of juveniles, as evidenced by the absence of changes in the hepatopancreas structure and absorptive capacity, and in the activity of digestive enzymes. These results confirm the high tolerance of the species to food deprivation. The present findings may reflect the potential ability of *C. quadricarinatus* juveniles to show compensatory growth in large-scale aquaculture systems. In addition, they are important from an economical point of view since they show that it is possible to significantly reduce the amount of food offered in culture systems, and consequently reduce production costs, without affecting juvenile survival and growth.

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