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Effect of intermittent feeding on growth in early juveniles of the crayfish *Cherax quadricarinatus*

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A B S T R A C T

Three experiments were conducted with juveniles of the crayfish *Cherax quadricarinatus* to investigate the effect of intermittent feeding regimes on growth and the ability to tolerate the shortage of food. In experiment 1, stage III juveniles were assigned to one of seven intermittent feeding groups (from FS1: 1 day fed/1 day non-fed to FS7: 7 days fed/7 days non-fed) and two control groups, continuously fed (CF) and continuously starved (CS) animals; this experiment comprised a short-term intermittent feeding period until the first molt, followed by a continuous feeding period. In the experiment 2, stage III juveniles were assigned to one of three intermittent feeding groups (FS2 to FS4) and one control group (CF); it consisted of a prolonged intermittent feeding period, until the end of the experiment. In the experiment 3, stage VI and VII juveniles were assigned to one of three intermittent feeding groups (FS2 to FS4) and one control (CF); it also consisted of a prolonged intermittent feeding period. The red claw crayfish juveniles were able to tolerate periods of intermittent feeding and underwent compensatory growth after continuous feed was re-established. The ability of crayfish to tolerate intermittent feeding was influenced by developmental stage and duration of the intermittent feeding period. Stage III juveniles survived, but decreased growth, when subjected to prolonged intermittent feeding. However, they showed full compensatory growth when the intermittent feeding period was short and followed by continuous feeding. On the other hand, stage VI–VII tolerated 60 days of prolonged intermittent feeding without any change in growth and survival. The hepatosomatic index (based on wet weight) values of the treatments and the control were similar, suggesting that intermittent feeding may not be considered a nutritional stress condition. The relative pleon weight (based on wet weight) values of the treatments and control were similar suggesting low use of nutrients from the muscle to increase the chance for survival. The juveniles of *C. quadricarinatus* can tolerate relatively long periods of low food availability and this is an important adaptation for their survival in changing/unpredictable environments and an attribute favorable for the production of the species.

1. Introduction

Variations in food availability are especially pronounced in freshwater environments, high latitudes and between groundwater and surface water ecosystems (Anger et al., 2004; Jalihal et al., 1993; Mezek et al., 2010). Food limitation may affect the survival of species and these can develop adaptations as a survival strategy (Mezek et al., 2010). The nutritional stress selects for an enhanced maternal energy investment into egg production, allowing a partially food-independent early larval development (Anger, 2001, 2006) and for abbreviated or direct developmental modes (Jalihal et al., 1993).

In addition, many animals have the capacity to compensate for weight loss, after a period of food deprivation (Li et al., 2005). Taking advantage of compensatory growth is one potential way to reduce costs and its use in aquaculture has been proposed as a tool to increase growth and improve food conversion efficiency (Foss et al., 2009; Hagen et al., 2009). The degree of compensatory growth is highly dependent not only on the species but also on the length and intensity of food deprivation (Hagen et al., 2009; Oh et al., 2008; Palma et al., 2010).

Decapod crustaceans also have the ability to tolerate starvation periods (Calado et al., 2007; Figueiredo et al., 2008; Gebauer et al., 2010; Wen et al., 2006) and to achieve compensatory growth after food restriction (Li et al., 2009; Singh and Balange, 2007; Wu et al., 2000, 2001; Wu and Dong, 2002a, b). *Fenneropenaeus chinensis* juveniles fed a low-protein diet showed compensatory growth after increasing dietary protein (Wu and Dong, 2002a). In addition, juveniles of this species produced a compensatory response when they were initially starved

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and then refed (Wu et al., 2000; Wu and Dong, 2002b) or exposed to different feeding levels and then refed ad libitum (Wu et al., 2001). *Macrobrachium nipponense* underwent compensatory growth after different periods of starvation followed by refeeding (Li et al., 2009). On the other hand, the effect of intermittent feeding on growth has been rarely evaluated (Mazlum et al., 2011; Wu and Dong, 2001; Zheng et al., 2008).

Feed cost represents a large portion (up to 80%) of total operating cost in intensive aquaculture (Thompson et al., 2010). For that reason, food restriction without effect on growth may be seen as an alternative strategy to reduce costs and increase profits of aquaculture operations (Bavčević et al., 2010). However, questions arise as to what extent should feeding rate be reduced without compromising the growth performance of the animals (Nunes et al., 2006).

Cherax quadricarinatus is an important species of freshwater crustacean for aquaculture. This species has been the subject of many studies concerning growth and nutrition (Campaña-Torres et al., 2008; Cortés-Jacinto et al., 2003, 2004a, b, 2005; Hernández-Vergara et al., 2003; Meade and Watts, 1995; Thompson et al., 2006; Villarreal-Colmenares, 2002). *C. quadricarinatus* has direct development and the first two lecithotrophic juvenile stages (JI and JII) stay with their mothers for 10 to 15 days (Levi et al., 1999). After molting to stage juvenile III (JIII) they become more independent from their mothers beginning the exogenous feeding (Levi et al., 1999). Following stages (III, IV and V) last approximately 10 days for each one and according to this, after 30 days juveniles are found in stage juvenile V or VI (Stumpf et al., 2010).

Recently, Stumpf et al. (2010) demonstrated that juveniles JIII can tolerate and compensate for a short period of intermittent feeding. Thus, the objective of this work was to evaluate the effect of short and long-term intermittent feeding on growth and survival at different stages of development of juveniles of the red claw crayfish, *C. quadricarinatus.*

2. Materials and methods

2.1. Animals

Juveniles of the crayfish *C. quadricarinatus* were obtained under laboratory conditions from reproductive stocks supplied by the farm Las Golondrinas (Entre Ríos) in Argentina. Ovigerous females weighing between 57 and 64 g were placed individually into 30-l glass aquaria (37 × 27 × 18 cm) containing a PVC tube (10 cm in diameter and 25 cm long) as shelter (Vazquez and López Greco, 2007), and dechlorinated water (pH 7–8, hardness 50–100 mg/l as $CaCO_3$ equivalents) under continuous aeration to maintain a dissolved oxygen concentration (DO) higher than 5 mg/l. The photoperiod was 14L:10D (Jones, 1997) and temperature was held constant at 27 ± 1 °C by ATMAN water heaters (100 W) (Jones, 1997). These females were fed daily ad libitum with *Elodea* sp. and commercial balanced food for tropical fish Tetracolor, TETRA® (Sánchez de Bock and López Greco, 2010; Stumpf et al., 2010; Vazquez et al., 2008). Juveniles were separated from their mothers after reaching the free-living stage III (Levi et al., 1999). Until the beginning of the experiments, they were fed a protein-rich diet and maintained under the conditions of water quality, temperature and photoperiod described above.

2.2. Experimental procedures

Three experiments were conducted. They comprised an intermittent feeding period followed or not by a continuous feeding period. The intermittent feeding period, consisted of alternating days of feeding and non-feeding.

In all the assays, each juvenile was carefully dried with a paper towel, weighed (initial weight) with an analytical balance (precision 0.1 mg) and randomly assigned to a single plastic container with water. The containers used for juveniles had a capacity of 500 cm^3 each, were filled with 300 ml of dechlorinated water and were provided with a 5 × 5 cm-synthetic net as shelter according to previous studies (Stumpf et al., 2010). During these experiments, the plastic containers were cleaned by siphoning and the water was totally renewed every day, in order to remove any food remaining. These water changes maintain levels of ammonia and nitrites undetectable, ensuring high water quality (Meade and Watts, 1995).

The water quality parameters were measured once a week in the water supply tank (200 L) for the experiments. These parameters, i.e. dissolved oxygen (5.4–8.0 mg l^{-1}), pH (7.3–8.4), hardness (60–100 mg l^{-1} as $CaCO_3$ equivalents) and temperature (26–29 °C) were within the ranges recommended for aquaculture (Boyd and Tucker, 1998; Jones, 1997). The photoperiod was 14L:10D (Jones, 1997).

On feeding days, animals were fed ad libitum once a day with Fundus® (Fideos Don Antonio SA), with a composition of crude protein 50.40%, crude fat 20.49%, 19.26% carbohydrates, 2.40% fiber and 6.82% moisture (Centro de Investigaciones Biológicas del Noreste, S.C. — Laboratorio de Analisis Químicos Proximales — México). This formulated food is a commercial trout diet and currently manufactured in Argentina and used in the crayfish culture.

2.2.1. Experiment 1: effects of a short-term intermittent feeding period followed by continuous feeding period on stage III juveniles

A total of 216 stage III juveniles with an average initial body weight of 17.01 ± 1.24 mg were randomly assigned to one of seven treatments and to one of two control groups (24 replicates). In this experiment, which lasted for 45 days, the intermittent feeding period was applied until molting to stage IV follows of the continuous feeding period until the end of experimental period, at day 45. The following treatments were performed: FS1 (1 day fed/1 day non-fed), FS2 (2 days fed/2 days non-fed), FS3 (3 days fed/3 days non-fed), FS4 (4 days fed/4 days non-fed), FS5 (5 days fed/5 days non-fed), FS6 (6 days fed/6 days non-fed) and FS7 (7 days fed/7 days non-fed). The controls consisted of CF (continuously fed) and CS (continuously starved) animals. These treatments were selected on the basis of previous results showing the best outcome for survival and growth (Stumpf et al., 2010).

2.2.2. Experiment 2: effects of a long-term intermittent feeding period on stage III juveniles

A total of 160 stage III juveniles with an average initial body weight of 16.78 ± 1.16 mg were randomly assigned to one of three treatments and to a control (40 replicates). The treated juveniles were subjected to intermittent feeding period until the end of the experiment at day 60. The following treatments were performed: FS2 (2 days fed/2 days non-fed), FS3 (3 days fed/3 days non-fed), and FS4 (4 days fed/4 days non-fed). The control was CF. These treatments were selected on the basis of the experiment 1 results.

2.2.3. Experiment 3: effects of a long-term intermittent feeding period on juveniles at stages VI and VII

A total of 96 juveniles with an average initial body weight of 0.36 ± 0.05 g (stages VI and VII) were randomly assigned to one of three treatments and to a control (24 replicates). The treated juveniles were subjected to intermittent feeding period until the end of the experiment at day 60. The following treatments were performed: FS2 (2 days fed/2 days non-fed), FS3 (3 days fed/3 days non-fed), and FS4 (4 days fed/4 days non-fed). The control was CF.

2.3. Calculations and data analysis

Molts and deaths were checked twice a day (morning and afternoon). Juveniles were weighed after molting to stage IV and at days 15, 30 and 45 (experiment 1). In the experiments 2 and 3 juveniles were weighed at days 15, 30, 45 and 60. The duration of stage III and percentage of individuals that survived after reaching stage IV (successful molting) were determined in experiment 1. At the end of all experiments, survival (S) and number of molts (NM) were calculated. In addition, all crayfish were sacrificed and their hepatopancreas and abdominal muscle were removed and weighed.

Initial and final wet weights of juveniles (W_I and W_F, respectively) were used to calculate growth increment from the equation: GI (%) = 100 × ((W_F − W_I) / W_I), and specific growth rate from the equation: SGR (%/day) = 100 × (ln W_F − ln W_I)/t, where t the number of days elapsing between weightings. The hepatosomatic index was determined on wet basis from the equation: HSI (%) = hepatopancreas wet weight / whole body weight 100 and the relative wet pleon weight from the equation: (RPW %) = pleon wet weight/whole body weight 100.

The independence between survival or first molt and treatments was tested using the Chi-square test of independence, followed by Fisher's test for multiple comparisons between treatments and CF (Zar, 1999). The parametric tests were applied when the assumptions of normality and homoscedasticity were met; otherwise, equivalent non-parametric tests were used. One-way ANOVA or the non-parametric Kruskal–Wallis test were used to test for differences in the number of molts (NM), the duration of stage III, and the percentages of GI, HSI and RPW among treatments. Repeated-measures ANOVA was used to test for differences in weight among treatments and two-way ANOVA was used to test SGR. The Dunnett's or the non-parametric Mann–Whitney tests were used for multiple comparisons between treatments and CF (Zar, 1999).

3. Results

3.1. Experiment 1: effects of a short-term intermittent feeding period followed by continuous feeding period on stage III juveniles

The percentage of juveniles that molted to stage IV was significantly lower ($p<0.05$) for CS (no molts) and FS1, with 50% of the juveniles being able to molt successfully (Fig. 1a). Intermittent feeding also affected the duration of stage III, which was longer for FS1, FS3 and FS7 ($p<0.05$) than CF (Fig. 1b). Despite the delay in reaching stage IV, no significant differences in the number of molts (NM) were found between these treatments and CF at day 45 of the experiment (Table 1, experiment 1).

There were no significant differences ($p>0.05$) in survival between treatments and CF at day 45 of the experiment, except for CS, which had a mortality of 100% within 13 ± 3 days of the experiment (Table 1, experiment 1).

Juveniles fed for 4–5 days during the intermittent feeding period showed similar growth at the end of this period in comparison with those in CF, except for FS4, with significantly lighter ($p<0.05$) juveniles (Fig. 2a). The value of GI was also lower for FS4 than for CF (Table 1, experiment 1). The average weight of FS4 was lower than that of CF during the intermittent feeding period but this weight loss was recovered by continuous feeding.

During the continuous feeding period, the final weights of the juveniles in all treatments were not significantly different from that of CF ($p>0.05$) (Fig. 2a). No significant differences in GI were observed between treatments and CF for at the end of this period (Table 1, experiment 1). No significant differences in SGR were found between treatments during the continuous feeding period, but that of FS4 was slightly higher within the first days of this period ($p>0.05$) (Fig. 2b). There were no significant differences in HSI and RPW among treatments ($p>0.05$) (Table 1, experiment 1).

3.2. Experiment 2: effects of a long-term intermittent feeding period on stage III juveniles

Number of molts (NM) was significantly lower in animals submitted to feed intermittent than in those submitted to continuous feed (CF) at

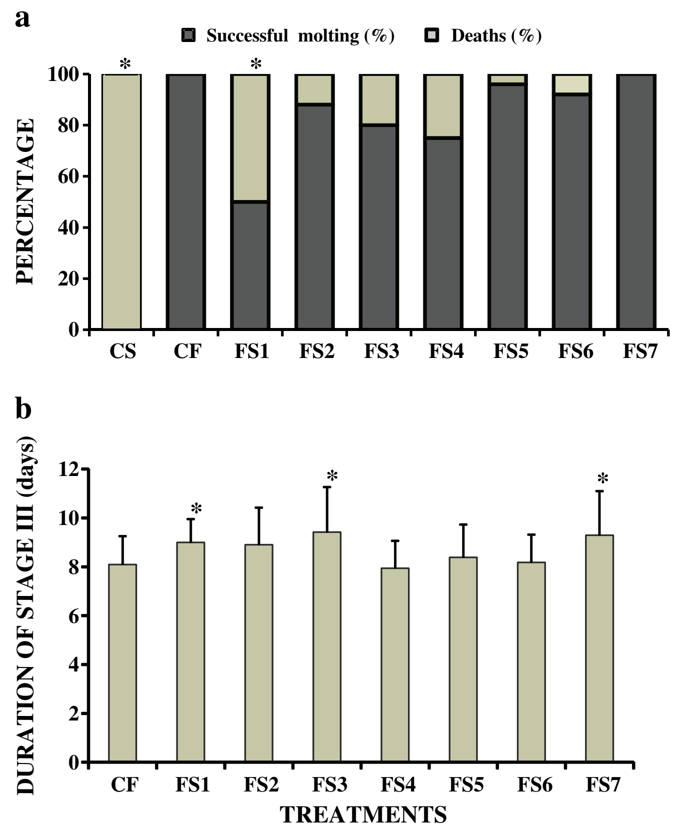

Fig. 1. (a) Percentage of juveniles that molted to stage IV obtained under different feeding treatments (experiment 1). (b) Duration of stage III (mean ± SD) during the intermittent feeding period (experiment 1).

day 60 of the experiment ($p<0.05$) (Table 1, experiment 2). Survival was not affected by the prolonged intermittent feeding ($p>0.05$) (Table 1, experiment 2).

Final wet body weight was significantly affected by the intermittent feeding period, being that differences were observed after 30 days of the experiment ($p<0.05$) (Fig. 2c). At day 60 of the experiment, no significant differences were observed among the weights of FS2, FS3 and FS4; however, these differed significantly from that of CF ($p<0.05$), with ~50% less weight than that of the control.

On average, the wet weight of crayfish subjected to CF was increased to 1677 ± 595% and that subjected to the other treatments increased ~750% (Table 1, experiment 2). No significant differences in HSI ($p>0.05$) were found between the treatments and the control and the RPW of FS2 was significantly lower than that of CF ($p<0.05$) (Table 1, experiment 2). During the experiment there were differences in SGR of crayfish for FS2, FS3 and FS4 than for CF ($p<0.05$), but in the last 15 days of the experiment, they did not differ ($p>0.05$) (Fig. 2d).

3.3. Experiment 3: effects of a long-term intermittent feeding period on juveniles at stages VI and VII

No significant differences ($p>0.05$) were found between treatments and CF at day 60 of the experiment in regard to wet body weight (Fig. 2e), specific growth rate (Fig. 2f), growth increment, survival, number of molts, hepatosomatic index and relative pleon weight (Table 1, experiment 3). On average, the weight of all juveniles increased 219–273% of the initial weight, survival was close to 100%, animals undergone ~3 molts, hepatosomatic index was ~12% and pleon was ~30% of total weight (Table 1, experiment 3).

Table 1
Effect of feeding treatments on growth parameters on juveniles of *Cherax quadricarinatus* in all experiments.

Treatments	At the end of intermittent feeding period		At the end of continuous feeding period					
	Feeding days	GI (%)[a]	Feeding days	GI (%)[b]	Survival (%)	NM	HSI (%)	RPW (%)
Experiment 1								
CS	0	–	0	–	0	0	–	–
CF	8	51.4 ± 9.6	37	395.0 ± 199.9	54	4.6 ± 0.5	9.8 ± 2.3	32.5 ± 5.1
FS1	4	48.7 ± 11.9	36	387.7 ± 138.9	37	4.2 ± 0.4	11.9 ± 1.6	35.7 ± 6.2
FS2	5	48.4 ± 11.5	36	441.0 ± 166.5	58	4.4 ± 0.7	10.6 ± 2.2	34.0 ± 3.6
FS3	5	51.4 ± 12.0	36	351.8 ± 197.3	54	4.2 ± 0.4	10.6 ± 2.3	35.6 ± 8.6
FS4	4	37.4 ± 16.3*	37	509.2 ± 185.7	42	4.5 ± 0.5	9.6 ± 2.0	31.0 ± 2.9
FS5	5	45.0 ± 9.3	37	413.3 ± 163.8	33	4.6 ± 0.5	9.5 ± 1.6	37.8 ± 4.2
FS6	6	46.8 ± 13.3	37	295.6 ± 135.3	37	4.3 ± 0.5	11.4 ± 1.6	37.1 ± 3.2
FS7	7	56.4 ± 9.7	36	453.1 ± 165.4	71	4.3 ± 0.5	10.7 ± 2.0	37.2 ± 4.6
At the end of intermittent feeding period								
Treatments			Feeding days	GI (%)[c]	Survival (%)	NM	HSI (%)	RPW (%)
Experiment 2								
CF			60	1677 ± 595.0	58	6.0 ± 0.7	11.0 ± 1.7	36.9 ± 3.1
FS2			30	798.5 ± 296.0*	75	4.5 ± 1.3*	11.0 ± 2.6	34.1 ± 4.4*
FS3			30	794.0 ± 381.0*	75	5.0 ± 0.8*	12.7 ± 3.3	37.1 ± 3.9
FS4			32	633.3 ± 255.9*	60	5.0 ± 0.8*	12.5 ± 2.4	34.2 ± 4.7
At the end of intermittent feeding period								
Treatments			Feeding days	GI (%)[c]	Survival (%)	NM	HSI (%)	RPW (%)
Experiment 3								
CF			60	272.7 ± 90.8	100	3.0 ± 0.5	8.9 ± 1.7	30.7 ± 2.6
FS2			30	249.2 ± 64.4	92	2.8 ± 0.5	8.9 ± 1.6	31.6 ± 2.6
FS3			30	273.5 ± 82.5	96	3.0 ± 0.4	8.4 ± 1.4	31.3 ± 2.3
FS4			32	219.1 ± 60.3	100	2.7 ± 0.5	8.9 ± 1.6	32.0 ± 2.8

NM: number of molts (accumulated). HSI: hepatosomatic index. RPW: relative pleon weight. CF (continuously fed), CS (continuously starved), FS1 (1 day fed/1 day non-fed), FS2 (2 days fed/2 days non-fed), FS3 (3 days fed/3 days non-fed), FS4 (4 days fed/4 days non-fed), FS5 (5 days fed/5 days non-fed), FS6 (6 days fed/6 days non-fed) and FS7 (7 days fed/7 days non-fed). Asterisk (*) indicates significant differences ($p < 0.05$) between each feeding treatment and the continuously fed control (CF).
[a] Growth increment after molting to stage IV.
[b] Growth increment between molting to stage IV and day 45 of the experiment.
[c] Growth increment after 60 days of experiment.

4. Discussion

Results showed that the red claw crayfish juveniles were able to tolerate short intermittent feeding period and underwent compensatory growth after continuous feeding is re-established. In addition, advanced juveniles can survive for long intermittent feeding periods and achieve similar weight as continuously fed animals. Thus, the ability of crayfish to tolerate intermittent feeding was influenced by the developmental stage and the duration of the intermittent feeding period.

The length of intermittent feeding over the 60-days had a significant impact on growth but not in the survival in stage III juveniles. On the other hand, stages VI–VII tolerated 60 days of intermittent feeding without any change in growth and survival. This high tolerance to alternate days of feeding and non-feeding may be an adaptive strategy to deal with changing environments and may be evolved during the freshwaterization process of the species (Jalihal et al., 1993).

There was a reduction of nearly 50% in the amount of food provided within 2 months of the study, (experiments 2 and 3) with excellent results in growth and survival and in this sense this could be an interesting tool to diminish production costs.

The stage III juveniles molted to the next stage and reach a weight comparable to the control with only 4 feeding days (Table 1, experiment 1). This is consistent with the information provided by Stumpf et al. (2010) which estimated that 3.5 days are necessary to achieve the point of reserve saturation (PRS_{50}). Small differences in survival, duration of stage III and growth increment of some treatments were found when comparing the experiment 1 with Stumpf et al. (2010) that could be caused for the different diets among assays. Altogether, the results of experiment 1 (present study) and Stumpf et al. (2010) demonstrate that juveniles stage III of *C. quadricarinatus* can fully compensate when the continuous feeding was reestablished.

There is little information available on compensatory growth in crayfishes. Gu et al. (1996) observed that *C. quadricarinatus* juveniles (130 mg) exposed to 12 days of food deprivation and refed for 6 days increased growth although this increase was not sufficient to achieve similar weight with respect to the control. Similar results were reported by Powell and Watts (2010) in *Procambarus clarkii* and *Procambarus zonalangus* adults with food deprivation for 5 months and refeeding for 1 month.

The increased intermittent feeding period in the experiment 2 did not affect the survival, however those juveniles molted less than the control. Maybe "saving" the energy required for molting is a strategy to tolerate food deprivation in the freshwater environment; consequently the intermittent feeding impacted on crayfish growth. Mazlum et al. (2011) indicated that when food is offered every 3 or 4 days to the juvenile crayfish *Astacus leptodactylus* growth is affected mainly by regulating molting frequency.

Juveniles of *C. quadricarinatus* that recently became independent from their mothers are known to be particularly vulnerable to nutritional deficiency because they reach stage III with few reserves of energy (García-Guerrero et al., 2003; Stumpf et al., 2010). Probably this vulnerability can also explain their lower growth when they were exposed to longer periods of intermittent feeding. In contrast, juvenile stages VI–VII were able to tolerate for a long period of intermittent feeding growing at a normal rate. This suggests that the vulnerability to food deprivation decrease throughout ontogenetic development during juvenile phase but further research is needed to clarify this issue.

To prevent damage or death, animals exposed to food deprivation present different strategies such as hibernation, reduction in metabolic

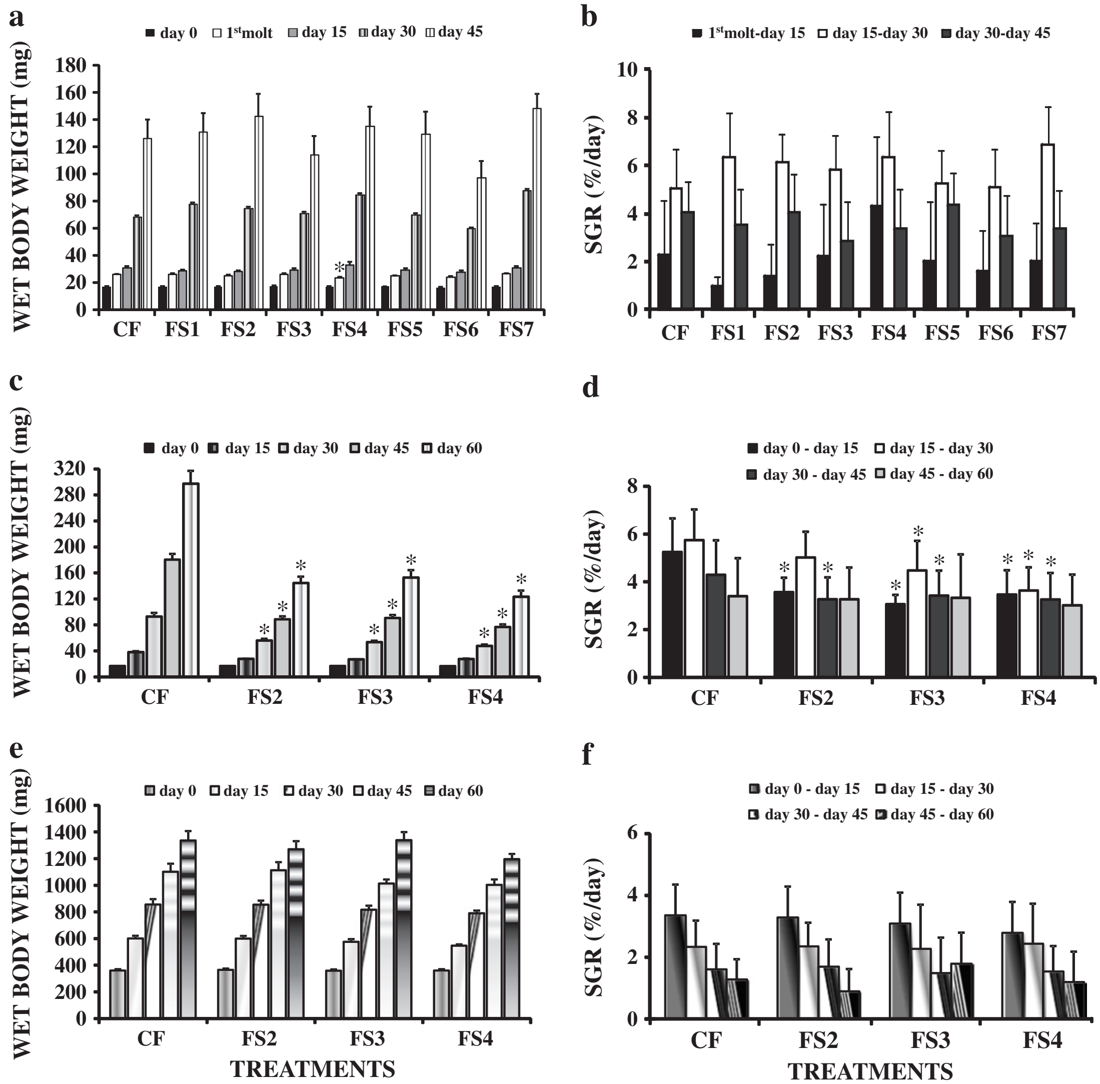

Fig. 2. (a) Wet body weight (mean ± SE) of juveniles during the experiment 1 and (b) specific growth rate (SGR; mean ± SD) during the continuous feeding period (experiment 1). (c) Wet body weight (mean ± SD) of juveniles and (d) specific growth rate (SGR; mean ± SD) during the experiment 2. (e) Wet body weight (mean ± SE) and (f) specific growth rate (SGR; mean ± SD) during the experiment 3. CF (continuously fed), FS1 (1 day fed/1 day non-fed), FS2 (2 days fed/2 days non-fed), FS3 (3 days fed/3 days non-fed), FS4 (4 days fed/4 days non-fed), FS5 (5 days fed/5 days non-fed), FS6 (6 days fed/6 days non-fed) and FS7 (7 days fed/7 days non-fed). Asterisk (*) indicates significant differences ($p<0.05$) between each feeding treatment and the continuously fed control (CF).

rate and/or increased mobilization of nutrient reserves (Sánchez-Paz et al., 2007). The HSI is used to evaluate the nutritional status and as an indicator of stress in crustaceans (Jussila and Mannonen, 1997). A decrease in this index could be expected during starvation conditions since the nutrients stored in the hepatopancreas are mobilized to meet the energy demands (Comoglio et al., 2005; Sureshkumar and Kurup, 1999).

In the present study the HSI was similar in the treatments and CF of all experiments suggesting that intermittent feeding at the assayed periods does not exert an effect of nutritional stress. Jones and Obst (2000) evaluating the effects of long starvation and refeeding in *Cherax destructor* observed that the hepatosomatic index calculated based on dry hepatopancreas weight was more efficient to detect alterations in the organ than that the HSI based on wet weight. Meanwhile, studies to assess food deprivation and consequently growth compensatory in crustacean are generally based on wet weight (Singh and Balange, 2007; Wu et al., 2000, 2001; Zhang et al., 2010).

The RPW did not differ from CF in all treatments except for FS2 of the experiment 2 (Table 1) which had a lower value. This could indicate some nutrient mobilization from this tissue to meet energy requirements. Powell and Watts (2010) evaluating the effects of a long starvation period in *P. clarkii* and *P. zonalangus* observed differences in the dry tail muscle weight, even after 1 month of refeeding. In addition, these authors observed in *P. clarkii* that the wet and dry total body weight of the crayfishes did not differ during the first 2 months of starvation but differed in the following months, even after the refeeding period. Meanwhile, wet and dry weights of *P. zonalangus* differed at the end of the first month of starvation and these differences continued until the end of the experiment. During starvation, energy is derived solely from endogenous resources, and tissues are lost due to catabolic activities. To maintain the necessary body volume and internal turgidity during starvation, the lost tissue mass must be replaced by water (Dall, 1974; Stuck et al., 1996; Wilcox and Jeffries, 1976). In *Litopenaeus vannamei* the most pronounced responses to starvation observed is a significant increase in water content and a corresponding decrease in the percentage of dry weight (Stuck et al., 1996).

Therefore, in the our study changes in the depletion of protein, glycogen and lipid reserves of the hepatopancreas and pleon would be required to complement the information of nutritional stress and to elucidate the mechanisms related with the intermittent feeding in *C.*

quadricarinatus. Histological analyses of the hepatopancreas also would be required to complement this study toward a better understanding of the changes in cellular composition and structure.

5. Conclusion

The present study has demonstrated that juvenile *C. quadricarinatus* can tolerate relatively long periods of low food availability. This is an important adaptation for their survival in changing environments and an attribute favorable for the production of the species. In addition, this study corroborated the ability to recover completely from short periods of food deprivation in the early stage of development. Advanced juveniles subjected to intermittent feeding regimes of 2–4 days have the same survival and mass gain as daily fed individuals. Currently, intermittent feeding practices are not utilized commercially by crustacean's farmers in this species. In semi-intensive culture where natural productivity in the pond may have satisfied part of the protein requirements of the red claw, the use of intermittent feeding protocols under an adequate stocking density could be a good strategy to diminish costs due to the reduction of the use of formulated feeds.

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