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NUTRITIONAL VULNERABILITY IN EARLY STAGES OF THE FRESHWATER ORNAMENTAL "RED CHERRY SHRIMP" *NEOCARIDINA DAVIDI* (BOUVIER, 1904) (CARIDEA: ATYIDAE)

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A B S T R A C T

This study evaluated the starvation resistance of the shrimp *Neocaridina davidi* during the first and the third juvenile stages (named here as JI and JIII) by means of the estimation of point-of-no-return (PNR_{50}). Two experiments were conducted with increasing numbers of days without food and two controls (one with continuous feeding, CF; the other, with continuous starvation, CS). Time to the first molt and number of molts did not differ among the treatments beginning at JI or JIII. Nevertheless, longer periods of starvation influenced growth and survival of juveniles beginning the starvation as JI, but these effects were not observed in JIII. The estimated values of PNR_{50} for JI and JIII were 16.15 ± 0.31 and 9.44 ± 0.26 days, respectively. The early stages of the life cycle are more tolerant to starvation than other decapods previously studied. Such ability indicates a great potential of this species for aquaculture.

KEY WORDS: aquaculture, cherry shrimp, freshwater, point of-no-return

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INTRODUCTION

The aquaculture production of numerous species has increased considerably since 2000, with crustaceans representing 10% of this production in 2012 (FAO, 2014). Many species of freshwater shrimp have been the focus of the aquarium trade (Lukhaup, 2002; Werner, 2003), including at least 18 species of the genera *Atya* Leach, 1816, *Atyopis* Chace, 1983, *Caridina* H. Milne Edwards, 1837; *Neocaridina* Kubo, 1938 and *Macrobrachium* Bate, 1868, regularly traded (De Grave et al., 2008). Besides being attractive for ornamental use, the laboratory culture of ornamental species contribute to reduce the impact from the wild collections and to develop small-scale productions (Calado et al., 2003; Calado, 2008).

Many species of the mentioned genera have abbreviated or direct post-embryonic development, facilitating their culture and thus resulting in a large increase in the production around the world.

The freshwater shrimp *Neocaridina davidi* (Bouvier, 1904) (red variety), popularly known as "red cherry shrimp," is sold from 1.5 to 3.5 cm of total length by 1 to 3 US/specimen (Turkmen and Karadal, 2012). Basic information on the biology of this species is still scarce in the literature. Investigations on the physiology of digestive trait among the few published studies (Wang et al., 2009, 2010), as well as, more recently, the effect of temperature on biochemical composition, growth and reproduction (Tropea et al., 2015) and a sustainable-low cost method for culture (Viau et al., 2015). The morphology of the initial post-hatching stages of *N. davidi*, obtained from females provided by the aquarist commerce, was recently studied by Pantaleão et al. (in press). Studies aimed at improving the feeding efficiency for growth of this species are necessary (Rodgers et al., 2006).

The nutritional vulnerability (Sulkin, 1978) or flexibility (Sulkin and Van Heukelem, 1980) in the early life cycle stages were studied in some decapods such as crabs (Anger, 1995; Harris and Sulkin, 2005; Figueiredo et al., 2008; Gebauer et al., 2010; Guerao et al., 2012), shrimp (Thessalou-Legaki et al., 1999; Paschke et al., 2004; Anger and Hayd, 2009, 2010; Zhang et al., 2009, 2014) and crayfish (Stumpf et al., 2010; Calvo et al., 2012).

At the larval or juvenile phase, nutritional vulnerability can be estimated by means of "point-of-reserve-saturation" (PRS) and "point-of-no-return" (PNR) (Anger and Dawirs, 1981). PRS represents the minimum time of initial feeding,

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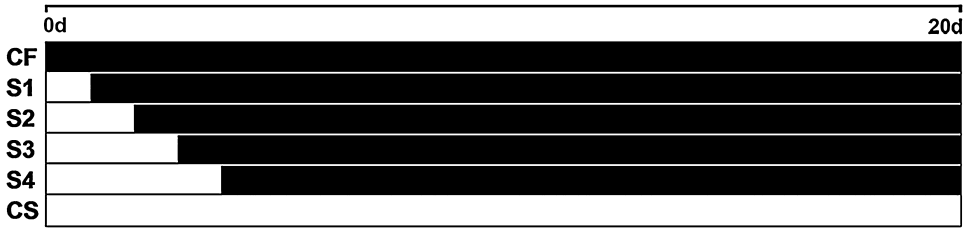

Fig. 1. Experimental design for the determination of the starvation resistance of the post-hatching stages (JI and JIII) of *Neocaridina davidi*. (■) Fed; (□) unfed. CF, continuously fed control; CS, continuously starved control; treatments; S1, S2, S3, S4, number after S = length of initial starvation period (days) (based on Paschke et al., 2004).

after which enough energy reserves have been accumulated for successful completion of a molting cycle, independent of later presence or absence of food. On the other hand, PNR represents the limit of time after which the individual loses the ability to recuperate from the nutritional stress caused by precocious starvation, even though followed by feeding *ad libitum* (Anger and Dawirs, 1981; Paschke et al., 2004; Gebauer et al., 2010).

Hence, to evaluate the immediate and later effects of early starvation on survival and growth in the early life cycle stages of ornamental species, such as *N. davidi*, PNR experiments are of fundamental importance to establish adequate protocols of feeding in their culture. This study evaluated the nutritional vulnerability of the red cherry shrimp from its early post-hatching stages (the first and the third juvenile stages named here as JI and JIII) by means of the estimation of point-of-no-return (PNR_{50}) with comparisons to other marine or freshwater species.

Material and Methods

Experimental Conditions for Producing Newly Hatched Individuals

Juveniles used in our experiments were obtained under laboratory conditions from breeding adults provided by local small scale aquarist breeders in the aquarium market. Two groups of reproducing adults with 20 females and 15 males were kept in plastic containers (25 cm × 32 cm × 15 cm) filled with 12 liters of dechlorinated freshwater (pH 7-8), under continuous aeration to keep the dissolved oxygen concentration at 5-8 mg/l, and photoperiod 14 L:10 D (Jones, 1997). The temperature was maintained at 27 ± 1°C provided by thermostat ATMAN (100 W). Java moss (*Vesicularia* sp.) was used as refuge in the containers. Adults were daily fed *ad libitum* with TetraColor (TETRA®), whose approximate composition is: 475 g/kg of protein, 65 g/kg of lipids, 20 g/kg of fiber, 60 g/kg of humidity, 15 g/kg of phosphorus and 100 mg/kg of ascorbic acid. This diet was previously tested and considered adequate to the species culture. Water from the bottom of the plastic containers was siphoned twice a week to remove the non-ingested food pieces and feces, and to exchange the water. The containers were daily checked for detecting ovigerous females, and the females carrying eggs were isolated in smaller plastic containers (21 cm × 14 cm × 15 cm) filled with 2 liters of freshwater. The females with embryos were kept under the same laboratory conditions as the reproducing adults until hatching.

Juveniles used in the experiments were the first (JI) and third post-hatching stages (JIII). Immediately after hatching, juveniles of the first stage (JI) were removed, counted and haphazardly distributed among the feeding treatments. Only broods with at least 18 individuals were used in the experiments. The individuals of the third post-hatching stage (JIII) were obtained from the same group of reproducing adults used in the experiment with JI. In order to obtain JIII we kept newly hatched individuals in the same container in which the two molts occurred; thereafter the juveniles were transferred and isolated for feeding restriction treatments. Furthermore, for the starvation experiments, samples of 10 juveniles (JI and JIII) from the same juvenile stock were conserved in ethyl alcohol (70%) for measurements of the cephalothorax length (CL), determined from the post-orbital angle to the posterior margin of the cephalothorax. The (CLI) was defined as the initial average size for each brood.

Experimental Conditions

The experiments consisted of juvenile exposure to different periods of initial starvation (starvation period), followed by continuous feeding (feeding period) until the end of each assay (Fig. 1). During the experiments, juveniles were kept individually in plastic containers (250 ml) filled with 200 ml of dechlorinated water (pH 7 to 8, hardness 70 to 100 mg l^{-1} as $CaCO_3$ equivalents) (200 ml). Those containers were arranged inside a plastic tray (53 cm × 40 cm × 12 cm) filled with freshwater maintained at 27 ± 1°C by thermostats ATMAN (100 W). Twice a week water volume was renewed in both experiments (JI and JIII), and the temperature was checked daily.

Starvation Experiments with the Early Stages (JI and JIII) of *N. davidi*

The effect of starvation on the survival and the ability to molt in individuals exposed to starvation from JI and from the third post-hatching stage (JIII) were tested in two experiments. In both experiments, 120 juveniles were randomly selected and initial CL measured (CLI ± SD = 0.83 ± 0.02 mm and 1.09 ± 0.02 mm of JI and JIII, respectively). Juveniles were assigned to the feeding treatments: two controls (CF, with continuous feeding; and CS, with continuous starvation) and four different periods of initial starvation (1, 2, 3 and 4 days, named S1, S2, S3 and S4), followed by continuous feeding until the end of the experiment, at day 20 (Fig. 1). Each treatment had 20 replicates (20 individuals from at least 5 different females). The duration of the experiments was based on a previous study (Barros-Alves et al., 2013).

Each day, food was offered *ad libitum* (1 pellet = 2.3 mg) (TetraColor TETRA®, see above for details), and food remains were removed the next morning. This protocol was based on previous studies developed by Stumpf et al. (2010) and Calvo et al. (2011, 2012) with juveniles of the freshwater crayfish *Cherax quadricarinatus* (von Martens, 1868). Juveniles were checked twice a day (morning and late afternoon) to record deaths and/or exuviae. At the end of the experiments, surviving individuals were preserved in ethylic alcohol (70%). The cephalothorax length was measured in order to estimate the final average size (CLF).

Statistical Analysis

Mortality was determined as the percentage of individuals in a given treatment that died before the end of the experiment. To estimate the PNR_{50} index, mortality was adjusted to the Boltzmann sigmoid model using the equation:

$$M = (a_1 - a_2)/(1 + e^{(b-x)/c}) + a_2,$$

where M is the percentage of mortality; a, b and c are constants, of which a_1 is the initial value, a_2 is the final value, b represents PNR_{50} and c is the time constant; and x is the independent variable represented by time of starvation (in days) (see Paschke et al., 2004; Bas et al., 2008; Gebauer et al., 2010; Calvo et al., 2012).

Parametric tests were applied when data met the model assumptions; otherwise, equivalent nonparametric tests were used. One-way ANOVA or the Kruskal-Wallis (test) were used to test differences in the CLI, CLF, number of molts (NM) and the time to occur the first molt (TM) among treatments, followed by Tukey's or Mann-Whitney (non-parametric) tests for multiple comparisons between treatments and the CF control. Mortality among groups was evaluated utilizing the 2-tailed Dunnett test with arcsine-transformed proportions (Zar, 2010). Statistical tests used in each experiment are indicated in the legends of Table 1 and Fig. 2. The level of significance was set at 5%.

Table 1. Post-hatching stages I and III of *Neocaridina davidi* (JI and JIII) exposed to different periods of starvation. In the JI experiment comparisons between treatments and continuously fed control (CF) made using one-way ANOVA followed by Tukey test. In the JIII experiment between treatments and continuously fed control (CF) made using Kruskal-Wallis test followed by Mann-Whitney test. * Significant differences ($p < 0.05$) observed between treatments and continuously fed control (CF). Means ± SD. CLI, cephalothorax length at the beginning of the experiment; CLF, cephalothorax length at the end of the experiment; NM, number of molts occurred up to 20 days of experiment; TM, time until the first molt.

Treatment	CLI (mm)	CLF (mm)	TM (days)	NM
Starvation experiment with JI				
CF	0.83 ± 0.02	2.09 ± 0.30	1.15 ± 0.36	7.10 ± 0.78
S1	0.81 ± 0.01	2.00 ± 0.28	1.55 ± 0.51	6.94 ± 1.10
S2	0.81 ± 0.01	2.08 ± 0.23	1.50 ± 0.51	7.00 ± 0.86
S3	0.82 ± 0.02	1.99 ± 0.21	1.10 ± 0.30	7.07 ± 0.86
S4	0.83 ± 0.02	1.75 ± 0.37*	1.00 ± 0.00	6.41 ± 1.08
CS	0.83 ± 0.02	1.40 ± 0.17*	1.20 ± 0.41	6.00 ± 0.57
Starvation experiment with JIII				
CF	1.09 ± 0.02	2.21 ± 0.21	2.05 ± 0.22	6.38 ± 0.60
S1	1.09 ± 0.03	2.25 ± 0.20	2.80 ± 0.69	6.30 ± 0.65
S2	1.09 ± 0.02	2.20 ± 0.17	2.65 ± 0.74	6.16 ± 0.65
S3	1.09 ± 0.02	2.18 ± 0.20	2.85 ± 0.81	5.81 ± 0.83
S4	1.09 ± 0.02	2.06 ± 0.27	2.70 ± 0.73	6.50 ± 0.81
CS	1.09 ± 0.02	–	2.60 ± 0.68	–

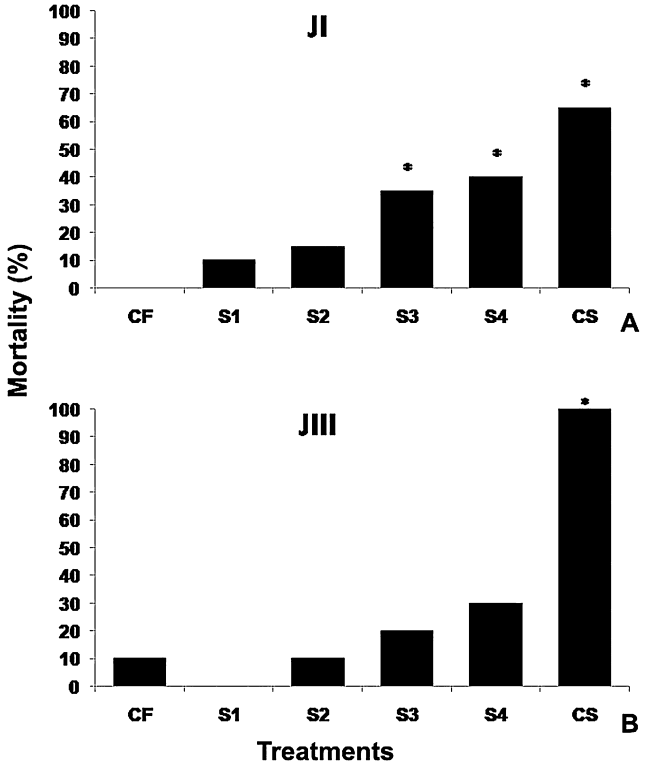

Fig. 2. Mortality estimated in starvation experiments with *Neocaridina davidi* post-hatching stages. A, juvenile stage 1; B, juvenile stage 3. * Significant differences ($p < 0.05$) in CF utilizing the 2-tailed Dunnett test with arcsine-transformed proportions.

RESULTS

Starvation Experiment with JI

At day 20, the final average carapace length (CLF) of juveniles from continuous feeding treatment (CF) was 2.09 ± 0.30 mm and this was significantly higher than S4 and CS treatments ($p < 0.001$) (Table 1). The time to occur the first molt (TM) in CF was 1.15 ± 0.36 days, while in CS was 1.20 ± 0.41 days; but there were no significant differences between CF and other treatments ($p = 0.991$) (Table 1). The number of molts (NM) was 7.10 ± 0.78 and 6.00 ± 0.57, for CF and CS respectively, with no significant differences between starvation treatments and CF ($p = 0.051$) (Table 1).

Mortality of juveniles was 0 and 65%, in CF and CS, respectively and it was statistically lower in CF when compared with treatments S3, S4 and CS ($p < 0.001$) (Fig. 2A). The PNR_{50} value estimated from the sigmoidal curve was 16.15 ± 0.31 days (Fig. 3A).

Starvation Experiment with JIII

The CLF of the CF individuals was 2.21 ± 0.21 mm, with no significant differences with those individuals that remained alive at day 20 in the treatments S1, S2, S3 and S4 ($p = 0.150$) (Table 1). Time to the first molt in CF was 2.05 ± 0.22 days, whereas in CS was 2.60 ± 0.68 days, with no significant differences between CF and other treatments ($p = 0.077$) (Table 1). CF individuals molted 6.38 ± 0.65 times and no significant differences were detected in NM among CF and survival juveniles at day 20 from S1 to S4 ($p = 0.076$) (Table 1). In CS treatment no juveniles survived until day 20.

The mortality measured in CF and CS was 10% and 100%, respectively, which is significantly different between these two treatments ($p < 0.001$) (Fig. 2B). The estimated PNR_{50} value was 9.44 ± 0.26 (Fig. 3B).

DISCUSSION

Starvation (PNR experiments; Anger and Dawirs, 1981) did not hinder the hatched juveniles' capacity to molt (NM), nor the time necessary to reach the first molt (TM) in either JI or JIII stages of *N. davidi*. These results suggest a high tolerance to starvation, presumably the highest already recorded in a decapod crustacean based on the recent revision by Calvo et al. (2012). Nevertheless, the periods of feeding restriction negatively affected growth and survival of

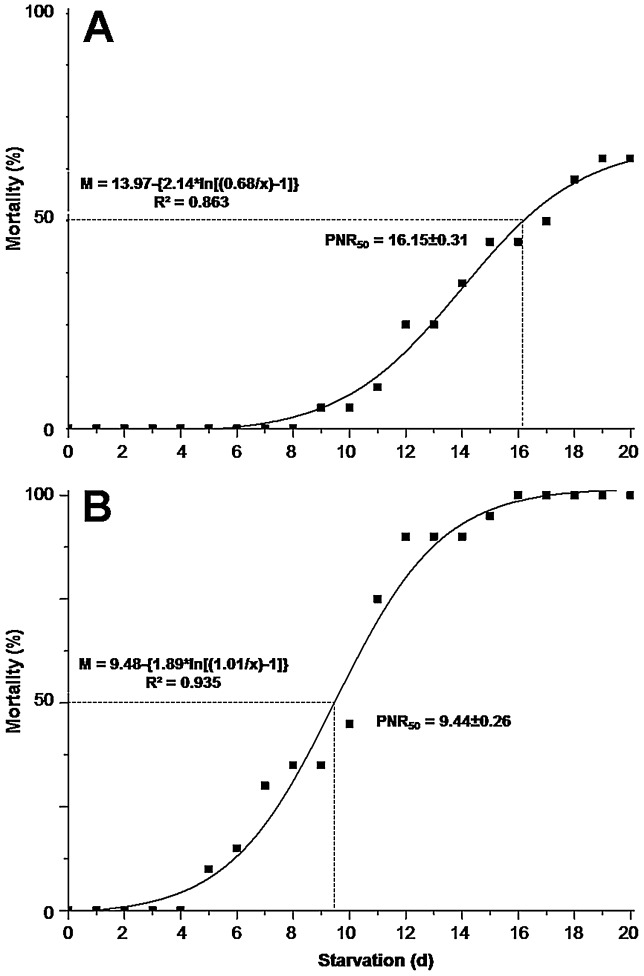

Fig. 3. Estimation of PNR_{50} in treatments with the same starvation periods for the post-hatching stages of *Neocaridina davidi*. A, juvenile stage 1; B, juvenile stage 3.

juveniles exposed to starvation immediately after hatching (JI).

The results obtained in *N. davidi*, which has a very abbreviated post-hatching development (Klotz et al., 2013; Pantaleão et al., in press), differed from those observed for marine species without abbreviated or direct post-embryonic development (Anger and Dawirs, 1981; Paschke et al., 2004; Calado et al., 2008; Gebauer et al., 2010). In such species the time necessary to reach the first molt was longer with an increasing period of restricted feeding, and none of those decapod species was able to molt in complete absence of food (CS).

In freshwater decapods, nutritional vulnerability has been studied in *Macrobrachium amazonicum* (Heller, 1862) having an extended larval development through 9 to 11 stages, similar to those in most estuarine and marine relatives (Anger and Hayd, 2009, 2010) while for species with abbreviated or direct post-embryonic development, information on nutritional vulnerability is only available for the crayfish *C. quadricarinatus* (Stumpf et al., 2010; Calvo et al., 2011, 2012). The effects of starvation are less harmful in *C. quadricarinatus* than in marine species. Nonetheless, for *C. quadricarinatus*, the time necessary to the first molt increased with the feeding restriction period, and no individual was able to molt when submitted to continuous starvation. This fact was also observed in other ontogenetic stages (first free-living stage and juveniles weighing 1 gram, Calvo et al., 2012). Thus, the early post-hatching stages of *N. davidi* are more tolerant to feeding restrictions than juveniles of *C. quadricarinatus*.

The value of PNR_{50} obtained in the present study was higher in the experiment with the individuals submitted to the treatments at JI than those submitted from JIII. Even without food (CS group) from time of hatching, JI survived longer than JIII similarly starved, which were fed along the two anterior post-hatching stages (JI and JII). This appears to be a suitable ecological adaptation for a hatching stage that may not find food immediately. However, JI individuals may be physiologically more robust to starvation than JIII, there were constraints for later survival and growth that did not occur in the experiment beginning with JIII individuals.

The fact that JI individuals of *N. davidi* have a large quantity of yolk in their cephalothorax region (energetic resources, Pantaleão et al., in press) might be the main reason for their survival for longer periods in the experiments, when compared to JIII. The higher period of survival of individuals exposed to starvation from JI may be due to a phenotypic plasticity of the species that allows utilization of the yolk during periods or places with low food supply. Anger (1995) observed such a fact studying another decapod, *Sesarma curacaoense* De Man, 1892. He also found that the first zoea of *S. curacaoense* contains a large quantity of yolk, but when food is available, the larva accumulates additional reserves of energy which can be advantageous in unpredictable nutritional conditions. In the same way early larval stages of *M. amazonicum* depend very little on food, shifting from completely non-feeding behaviour (zoea I) through facultative lecithotrophy (zoea II), to planktotrophy (later stages) (Anger and Hayd, 2009).

Besides PNR_{50}, there is another value commonly used to assess nutritional vulnerability, the PRS_{50} (point-of-reserve-saturation) (Anger and Dawirs, 1981). PRS is defined as the minimum time of initial feeding, after which enough energy reserves have been accumulated for successful completion of a larval molting cycle, independent of later presence or absence of food. PRS_{50} for *C. quadricarinatus* was estimated in 3.53 days at JIII, representing 36% of the total duration of this stage (Stumpf et al., 2010). The values of PRS_{50} may vary in different groups of decapods, as previously indicated in the literature (e.g., Anger, 1995; Liddy et al., 2003; Paschke et al., 2004). Taking into account that early post-hatching stages of *N. davidi* under continuous starvation (CS) can molt, we can assume that the value of PRS_{50} corresponds to zero. This value indicates complete independence of the food for molting in both experiments, JI or JIII, therefore no further assays appear necessary to evaluate PRS_{50}.

Gebauer et al. (2010) proposed an index to evaluate nutritional vulnerability (NVI, nutritional vulnerability index), defined as the quotient between PRS_{50} and PNR_{50}. The NVI increases with increasing of nutritional vulnerability, and decreases with decreasing dependence of food. The values of NVI can fluctuate from values slightly higher than zero to

infinity. Values near zero indicate that larvae are highly independent of exogenous food (for more details, see Gebauer et al., 2010). According to the present results, the NVI of *N. davidi* early stages corresponds to zero. This value was not found in any other decapod studied to date (see Table 3 from Gebauer et al., 2010), neither in *C. quadricarinatus*, a decapod species with direct development with low nutritional vulnerability with NVI values estimated at 0.24 for JIII and 0.18 for juveniles weighing 1 gram (Calvo et al., 2012).

Jalihal et al. (1993) assumed a set of features observed in species of the genus *Macrobrachium* Bate, 1868 were a result of a gradual evolution in the occupation of freshwater environments, which they named as "freshwaterization." Among those features were: the small size of the adults and the loss of sexual dimorphism; large size of eggs with proportional reduction of its number; advanced and large larvae with functional pereiopods and pleopods from hatching; high tolerance to feeding restriction; and regular periodicity in molt process. Most of these features are exhibited by the species studied here. Additionally Jalihal et al. (1993) mentioned that these features are favorable for aquaculture of these species. The results of this research in *N. davidi*, and those of the crayfish *C. quadricarinatus* (Stumpf et al., 2010; Calvo et al., 2012) reinforce the generalization not only for the genus *Macrobrachium* (Jalihal et al., 1993), but also for other decapod groups inhabiting landlocked freshwater habitats.

The high resistance to starvation showed by *N. davidi* gives the species a high potential to its aquaculture for the ornamental not only shrimp trade, but also is a characteristic of a viable invader in the Neotropical region. Calvo et al. (2012) suggested the NVI as an indicator to evaluate the invasive ability of a species; and, in this sense, this index indicates great tolerance to starvation for *N. davidi* (approximately zero). Some common features in invaders species include a fast growth, precocious maturation, high tolerance to environmental variations, and high ability to disperse (Boos et al., 2011). All of these features are found in the species studied in this paper and can be confirmed by its increasing use among commercial raisers and hobbyists for captive culture. Additionally, many atyid shrimps are small when compared to other freshwater shrimps, but very abundant in their original environment, such as little streams or lagoons where they occur (Wowor et al., 2004).

This study is the first contribution on the effect of starvation in Atyid species with abbreviated post-embryonic development. Thus, taking into account that the commercial culture of the Red Cherry Shrimp (*N. davidi*) is increasing exponentially worldwide, our findings provide not only essential information for aquaculture protocols of the species, but also contribute to some biological aspects of the early phase of its life cycle.

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