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Journal of Crustacean Biology

JOURNAL OF CRUSTACEAN BIOLOGY, 32(6), 883-890, 2012

INFLUENCE OF FEMALE SIZE ON OFFSPRING QUALITY OF THE FRESHWATER CRAYFISH *CHERAX QUADRICARINATUS* (PARASTACIDAE: DECAPODA)

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ABSTRACT

Knowledge on maternal influences in offspring quality of decapod crustaceans is limited, especially for freshwater species. We investigated the effects of female body weight on production variables (actual fecundity, AF), morphological/morphometrical features of eggs (volume, wet and dry weights) and recently independent juveniles (size, weight), and on juvenile growth performance and survival in the freshwater crayfish *Cherax quadricarinatus* (von Martens, 1868), under laboratory conditions. For this purpose, two groups of females were used: "large females" weighing 50-70 g; and "small females" weighing 20-35 g. The AF was the only production variable that increased with female weight. The percentage of ovigerous females also tended to increase with female weight: the 73% of "large females" and the 57% of "small females" spawned once. The remaining features did not vary with female weight. These results indicate that under controlled and constant laboratory conditions the egg and juvenile quality are similar between "small females" and "large females," an important outcome both from a theoretical and an economical point of view. In particular, this is the first report on the absence of correlation between maternal weight and juvenile size in a decapod crustacean with direct development. The results are compared with previous studies mainly in marine decapod species with indirect development.

KEY WORDS: decapod crustaceans, egg quality, female weight, juvenile quality, production variables

DOI: 10.1163/1937240X-00002103

INTRODUCTION

The term "offspring quality" refers both to the "egg quality" and the "larval/juvenile quality." The former is defined as the ability of an egg to be fertilized and undergo development (Holcomb et al., 2004), while the latter refers mainly to the physiological condition and growth performance of larvae/juveniles (Racotta et al., 2003). The offspring quality can be studied using morphological/morphometrical criteria, which include variables such as the weight and size of eggs and larvae/juveniles, and the production criterion, which includes parameters such as fecundity and rates of spawning, fertilization, and hatching.

In decapod crustaceans, offspring quality depends mainly on the physiological condition of the spawners, which is determined in turn by adult size, nutrition, and consecutive spawning, among others factors (Harlioğlu et al., 2002; Ramirez Llodra, 2002; Racotta et al., 2003; Smith et al., 2004; Rodríguez-González et al., 2006; Hoa et al., 2009; Wu et al., 2010). In relation to fecundity, which is usually measured in terms of number of eggs (realized fecundity), several authors have demonstrated an increase with female size in shrimp (Hansford and Marsden, 1995; Anger and Moreira, 1998; Ramirez Llodra et al., 2000; Thatje et al., 2004; Hernáez et al., 2008; Rólier Lara and Wehrtmann, 2009; Echeverría-Sáenz and Wehrtmann, 2011), anomurans (Sampedro et al., 1997; Litulo, 2005; Bueno and Shimizu, 2008; Hernáez and Wehrtmann, 2011), brachyurans (Pinheiro et al., 2000; Figueiredo et al., 2008; Pathre and Meena, 2010; Wehrtmann et al., 2010), and lobsters of the genus *Jasus* (Arana et al., 1985; Báez et al., 1985; Annala and Bycroft, 1987). The egg size, on the other hand, was found to be related to female size in some populations of the American lobster *Homarus americanus* Milne Edwards, 1837 (Attard and Hudon, 1987; Sibert et al., 2004), and in the European lobster *H. gammarus* Linnaeus, 1758 (Tully et al., 2001; Agnalt, 2008). However, knowledge on maternal size influence on offspring quality of decapod crustaceans is limited, since most studies focus only on production and egg morphological/morphometrical variables of species with indirect development.

Freshwater crayfish constitute an economically and ecologically important crustacean group with direct development. The relationship between offspring size and maternal influence is likely strongest and most consistent in this group because there is no larval stage that could affect (through either extended swimming or larval feeding) the relationship between juvenile energy reserves and original maternal provisioning (Marshall and Keough, 2008). Nonetheless, little is known about the effect of female size on offspring quality, with all the studies performed until now stating a correlation between maternal size and realized fecundity (Carral et al.,

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DOI:10.1163/1937240X-00002103

1994; Honan and Mitchell, 1995; Austin, 1998; Nakata and Goshima, 2004; Maguire et al., 2005; Kozák et al., 2006; Sáez-Royuela et al., 2006), and between maternal size and egg size in different crayfish species (Mason, 1978; Nakata and Goshima, 2004; Maguire et al., 2005). The possible influence of female weight on morphological/morphometrical features and growth performance of larvae has only been studied in marine species of crustacean decapods (Jørstad et al., 2005; Moland et al., 2010; Sato and Suzuki, 2010), with no available information for freshwater crayfishes.

The subject of the present study, *Cherax quadricarinatus* (von Martens, 1868), is a freshwater species with direct development: 9 embryonic stages and 2 post-hatching stages (juveniles I and II) have been described, all of which are attached to the pleopods of the mother, and feed on the yolk reserves accumulated in the eggs (embryo) or in the cephalothorax (juvenile I/II). The juvenile stage III (JIII) is the first stage independent from the mother that feeds exogenously (Levi et al., 1999; García Guerrero et al., 2003).

Although *C. quadricarinatus* is native to Australia and Papua New Guinea, its introduction to Argentina and many other countries for commercial purposes made the species distribution much wider (Medley et al., 1994; Rouse, 1995; Rodgers et al., 2006; Wicky et al., 2008). Due to the importance of this crayfish for aquaculture many aspects of its biology were investigated through experimental laboratory studies, which reproduce the controlled conditions of culture systems. From such laboratory studies it is known that females are capable of mating and spawn viable progenies in a weight range of 20-200 g (Yeh and Rouse, 1994; Curtis and Jones, 1995), and that fecundity increases with female size (King, 1993; Masser and Rouse, 1997; Austin, 1998). About 30% of the eggs are lost during incubation, according to Yeh and Rouse (1994) and Masser and Rouse (1997). Complementary laboratory studies analyzing the influence of maternal size on egg and juvenile quality of this species could aid our understanding of the reproductive output of freshwater decapods. The advantage of these studies over some of the investigations previously mentioned (field studies) is that those environmental variables that could influence offspring quality (temperature, food availability) are controlled and fixed, making it possible to determine the effect of the variable of interest (maternal size).

Based on these considerations, the objective of the present study was to investigate the effects of female body weight on the offspring quality of the freshwater crayfish *C. quadricarinatus* under controlled conditions.

Materials and Methods

Animals

The reproductive stock (36 females and 10 males) was obtained from the Farm Pinzas Rojas S.R.L., Tucumán, Argentina, and was acclimated to laboratory conditions for 1 month. During that period, females and males were placed separately into glass aquaria of 60 × 40 × 30 cm containing 30 l of dechlorinated tap water, under continuous aeration (pH 7.5, hardness 80 mg l^{-1} as $CaCO_3$ equivalents). The temperature was held constant at 27 ± 1°C by water heaters (100 W, precision 1°C), and the photoperiod was 14L:10D (Jones, 1997). Each aquarium was provided with PVC tubes (10 cm in diameter and 25 cm long) as shelters (Jones, 1995a). The animals were fed daily ad libitum with *Elodea* sp. and commercial balanced food for tropical fish – Tetracolor (Tetra holding, US), Inc. Blacksburg, Germany – with an approximate composition as follows: min. crude protein 47.5%, min. crude fat 6.5%, max. crude fiber 2.0%, max. moisture 6.0%, min. phosphorus 1.5% and min. ascorbic acid 100 mg kg^{-1}, which was demonstrated to be optimum for the species rearing under laboratory conditions (López Greco et al., 2007; Stumpf et al., 2010; Tropea et al., 2010).

Experimental Design

At the end of the acclimation period, the animals were weighed and non-ovigerous females were assigned to one of the following treatments according to their weight:

– *GROUP A*: "large females" = 15 females weighing 50-70 g (mean weight: 61.27 ± 4.50 g; mean post-orbital cephalothorax length: 45.29 ± 1.53 mm);
– *GROUP B*: "small females" = 21 females weighing 20-35 g (mean weight: 31.34 ± 3.11 g; mean post-orbital cephalothorax length: 34.11 ± 1.87 mm).

The female weights were selected taking into account that females with a weight similar to that of Group A are those commonly used as brooders in culture, while the weight of Group B corresponds to that from which females are capable of mating and produce viable progeny (i.e. onset of sexual maturity) (Curtis and Jones, 1995).

Three or four females from the corresponding group were stocked together with 1 male (weighing 70-90 g) for mating in a glass aquarium of 60 × 40 × 30 cm (16.7/20.8 animals/m^2), under the same conditions of water quality, temperature, photoperiod, and feeding as described above (García-Guerrero et al., 2003; Rodríguez-González et al., 2006). Males were selected based on similar body characteristics (similar body weight and chelae size, presence of both chelae with intact red patches) to discard a possible effect of male traits on female reproductive investment and offspring quality, as previously observed for other crayfish species (Galeotti et al., 2006; Rubolini et al., 2006; Aquiloni and Gherardi, 2008).

Four aquaria were used for the experimental group A and 6 for the experimental group B. All aquaria were cleaned and water was completely replaced once a week, when the animals were inspected to determine the presence of ovigerous females.

Once an ovigerous female had the eggs cemented to the pleopods, it was placed individually into an aquarium of 33.5 × 25 × 19 cm containing 8 l of dechlorinated tap water, under the same conditions described above. When the eggs reached a violet color [stage 6-7 of the embryonic development, according to García-Guerrero et al. (2003)], a sample of 10 eggs was removed from the first left pleopod of each female to evaluate the egg quality. The sample was weighed (wet weight; precision: 0.1 mg) and the individual egg weight was calculated by dividing the sample weight by the number of eggs. They were then measured under a stereomicroscope, and due to the elliptic shape of the eggs, the dorsal-ventral, anterior-posterior and right-left lengths were recorded. Finally, egg dry weights were determined (precision: 0.1 mg) following oven drying of the eggs at 60°C (to minimize volatilization of lipids at higher temperatures) to a constant weight (Hines, 1982).

After hatching, juveniles remained with their mothers until they reached the free-living stage III; at that time they were separated from the females and were counted.

Susequently, the quality of the juveniles was determined by means of the following procedure:

1. A sample of 40 juveniles III (JIII) was taken from each brood, and the body wet-weight (BW) was registered for each juvenile (precision: 0.1 mg). A mean value was calculated for the sample, so that each brood was a replicate.
2. Another sample of 10 JIII was taken from each brood, and the post-orbital cephalothorax length (POL) was measured from behind the eye to the end of the cephalothorax for each juvenile (precision: 0.01 mm). A mean value was calculated for the sample, so that each brood was a replicate.
3. Another sample of 12 JIII was taken from each brood to analyze survival and growth of juveniles throughout 2-3 stages beyond JIII stage (Growth Experiment), according to previous studies performed in shrimp and crab larvae (Bray and Lawrence, 1992; Hernández-Herrera et al., 2001; Wu et al., 2010). The animals were weighed (initial body weight: IBW) and then placed in individual containers of 500 cm^3 with a piece (4 × 4 cm) of onion bag mesh as shelter (Stumpf et al., 2010). The containers had continuous aeration and a water temperature of 27 ± 1°C. The juveniles were fed daily ad libitum with Tetracolor®, and water was completely replaced twice a week. Mortality was recorded daily. At the end of the experimental period (30 days) the animals were sacrificed and the final body weight (FBW) and POL were registered. A mean value of each variable was calculated for the sample, so that each brood was a replicate.

This procedure was performed only for the first spawns of "large females" and "small females," to eliminate a possible effect of consecutive spawning on offspring quality (Tropea, 2012). The experimental period comprised 150 days during the reproductive season of the species in Argentina (from August to March).

Statistical Analysis

The formulae used to calculate the different indices related to production variables were as follows:

1. Percentage of ovigerous females: OF = 100 × (number of ovigerous females/total number of females) (Wu et al., 2010).
2. Percentage of ovigerous females successfully hatched: OFH = 100 × (number of ovigerous females successfully hatched/total number of ovigerous females) (Wu et al., 2010).
3. Actual fecundity: AF = total number of JIII/female (Nhan et al., 2009; Wu et al., 2010).

The formulae used to calculate the different indices related to morphological/morphometrical variables of eggs and to the growth performance of juveniles were as follows:

a) Egg volume: $EV = 4/3 \times \pi \times r1 \times r2 \times r3$, where r1, r2 and r3 are the radios corresponding to the dorsal-ventral, anterior-posterior and right-left lengths, respectively (García-Guerrero and Hendrickx, 2006).
b) Specific Growth Rate for one month old-juveniles: $SGR = 100 \times ((\log_e FBW - \log_e IBW)/\text{time})$, where time was expressed in days (Jussila and Evans, 1997; Reynolds, 2002).
c) Growth Increment for one month old-juveniles: $GI = 100 \times ((FBW - IBW)/IBW)$ (Jones, 1995b).
d) Survival during the Growth Performance Experiment: the percentage of juveniles alive at the end of 5 day-long periods during 1 month (a total of 6 periods).

All the described indices were calculated for each brood (replicate), except OF and OFH, which were calculated for each treatment ("large females" and "small females"). Since the number of juveniles needed per brood to analyze all the variables mentioned was 62, those broods with less than 70 juveniles were not used for the experiment (but they were considered to calculate OF and OFH).

A one-way analysis of variance (ANOVA) (Sokal and Rohlf, 1995) was applied to compare between "large females" and "small females" all the morphometric variables (POL and EV) and weights (BW, dry and wet weight of the eggs) recorded, the indices calculated for one month old-juveniles (SGR and GI), and the production variable AF. OF and OFH were analyzed through the Fisher exact test (Sokal and Rohlf, 1995). Also, the following relationships were analyzed by linear regression: AF versus maternal weight; EV, egg wet weight and egg dry weight versus AF. For the former, the data were first converted to logarithms (base 10) to reduce heteroscedasticity, and the regression coefficient obtained was tested against the prediction of an allometric coefficient of 1.0 using Student's t-test (Sokal and Rohlf, 1995). The results per treatment are presented as mean ± SE according to Fotedar (2004). All tests were carried out at the 95% significance level.

RESULTS

Production Variables

Eleven broods were obtained in Group A ("large females") and twelve in Group B ("small females"). Two of these broods were discarded from the analysis for the reason mentioned in the previous section.

We plotted untransformed AF versus female weight is given in (Fig. 1A). "Large females" had higher AF than "small females" ($P < 0.05$; Table 1), with AF values ranging from 157 to 447 and from 113 to 249 JIII/female, respectively. The regression equation derived from log-transformed data was significant ($P < 0.05$), with a coefficient significantly lower than 1.0 ($P < 0.05$; Fig. 1B).

Also, OF tended to be higher in Group A, although this difference was not statistically significant ($P > 0.05$; Table 1). In both groups, 100% of the ovigerous females successfully hatched (Table 1).

Morphological/Morphometrical Variables

No statistical relationship was observed between (EV), egg wet weight and egg dry weight versus AF ($P > 0.05$; Fig. 2).

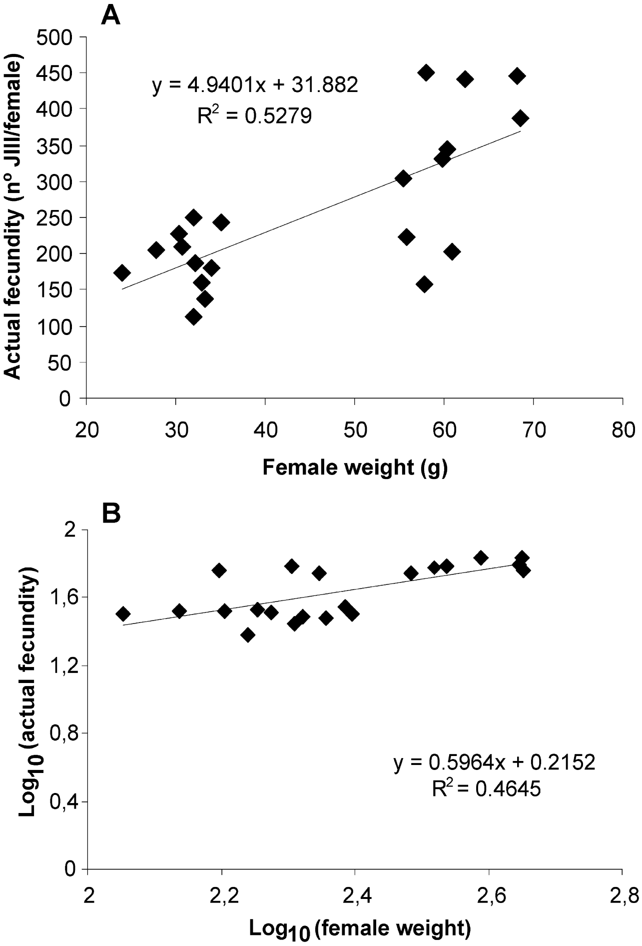

Fig. 1. Relationship between actual fecundity and female weight for the freshwater crayfish *Cherax quadricarinatus* (von Martens, 1868). A, untransformed, B, $\log_{10}$ transformed data (n = 21).

Table 1. Effect of maternal size on production variables and morphological/morphometrical variables of eggs, juveniles III and 1 month old-juveniles in the freshwater crayfish *Cherax quadricarinatus* (von Martens). The number of replicates (broods) used to calculate each variable value (except OF and OFH) was 11 for Group A ("large females") and 12 for Group B ("small females"). Values (mean ± s.e.) followed by the same letter are not significantly different ($P > 0.05$). AF = actual fecundity, BW = body weight, GI = growth increment, OF = percentage of ovigerous females, OFH = percentage of ovigerous females successfully hatched, POL = postorbital cephalothorax length, SGR = specific growth rate.

Parameter	Group A	Group B
Production variables		
SR (%)	73.33[a]	57.14[a]
SSR (%)	100[a]	100[a]
AF	328.70 ± 33.78[a]	189.64 ± 12.91[b]
Morphological variables		
Eggs		
Wet weight (mg)	5.15 ± 0.17[a]	5.15 ± 0.13[a]
Dry weight (mg)	2.26 ± 0.07[a]	2.29 ± 0.07[a]
Volume (mm^3)	6.50 ± 0.31[a]	6.47 ± 0.17[a]
Juveniles III		
BW (mg)	16.24 ± 0.32[a]	16.66 ± 0.52[a]
POL (mm)	3.28 ± 0.03[a]	3.29 ± 0.03[a]
1-month-old juveniles		
Survival (%)	36.67 ± 11.33[a]	64.29 ± 7.86[a]
BW (g)	123.46 ± 15.85[a]	117.59 ± 14.45[a]
POL (mm)	6.56 ± 0.23[a]	6.29 ± 0.27[a]
GI (%)	630.83 ± 94.23[a]	606.25 ± 75.41[a]
SGR (%/day)	6.33 ± 0.46[a]	6.32 ± 0.38[a]

These parameters, as well as the morphological features of the JIII (BW and POL), did not vary with female weight ($P > 0.05$; Table 1).

Finally, in the Growth Experiment a tendency was observed towards higher values of juvenile survival in broods of "small females" from day 10, although no statistical significance was found ($P > 0.05$; Fig. 3; Table 1). Both the growth indices (SGR and GI) and the morphological features of juveniles (POL and BW), were similar and independent of the mother weight ($P > 0.05$; Table 1).

Discussion

The production variables analyzed did not vary with female weight, except for the actual fecundity [AF, measured in terms of number of released juveniles (JIII)], which almost doubled in "large females" that of "small females." A similar result has been previously reported by Austin (1998), Truong et al. (2002) and Kozák et al. (2006) in the crayfishes *C. quadricarinatus*, *C. destructor* Clark, 1936, and *Orconectes limosus* (Rafinesque, 1817), respectively. In the present study, the value of regression coefficient was lower than 1, indicating the absence of a simple allometric relationship between AF and female weight. This suggests that the AF of larger females is proportionally lower compared to that of smaller females for the weight range of 20-70 g. The AF was more variable in "large females" than in "small females," a common observation in crustaceans (Somers, 1991). According to this result, female weight may be a better indicator of its reproductive potential (in terms of the number of JIII that it can produce) for the weight range of "small females."

With respect to the egg morphological/morphometrical features, Clarke (1993) has previously demonstrated a positive correlation between egg size and the level of nutrients stored in the eggs. These parameters are in addition easy and quick to assess; hence, they are generally considered as good indicators of egg quality (García-Ulloa et al., 2004). In the present study, egg volume and weight did not correlate with female weight and AF, with this result being the first report in a freshwater crayfish from Parastacidae. It would imply that the amount of the metabolic reserves transferred from the mothers to their eggs is a rather fixed parameter, independent both of female weight and the number of juveniles brooded. This seems to be the general trend in several species of shrimp (Wehrtmann and Lardies, 1999), crabs (Hines, 1991; Rabalais, 1991; DeMartini and Williams, 2001; Sato and Yoseda, 2008; Wehrtmann et al., 2010) and crayfish from Astacidae and Cambaridae (Abrahamsson, 1971; Skurdal and Qvenild, 1986; Harlioğlu and Türkgülü, 2000; Nakata et al., 2004; Kozák et al., 2006; Sáez-Royuela et al., 2006). However, in the European lobster *H. gammarus* (Tully et al., 2001; Jørstad et al., 2005; Agnalt, 2008; Moland et al., 2010), the freshwater crayfish *Austropotamobius torrentium* (Schrank, 1803)

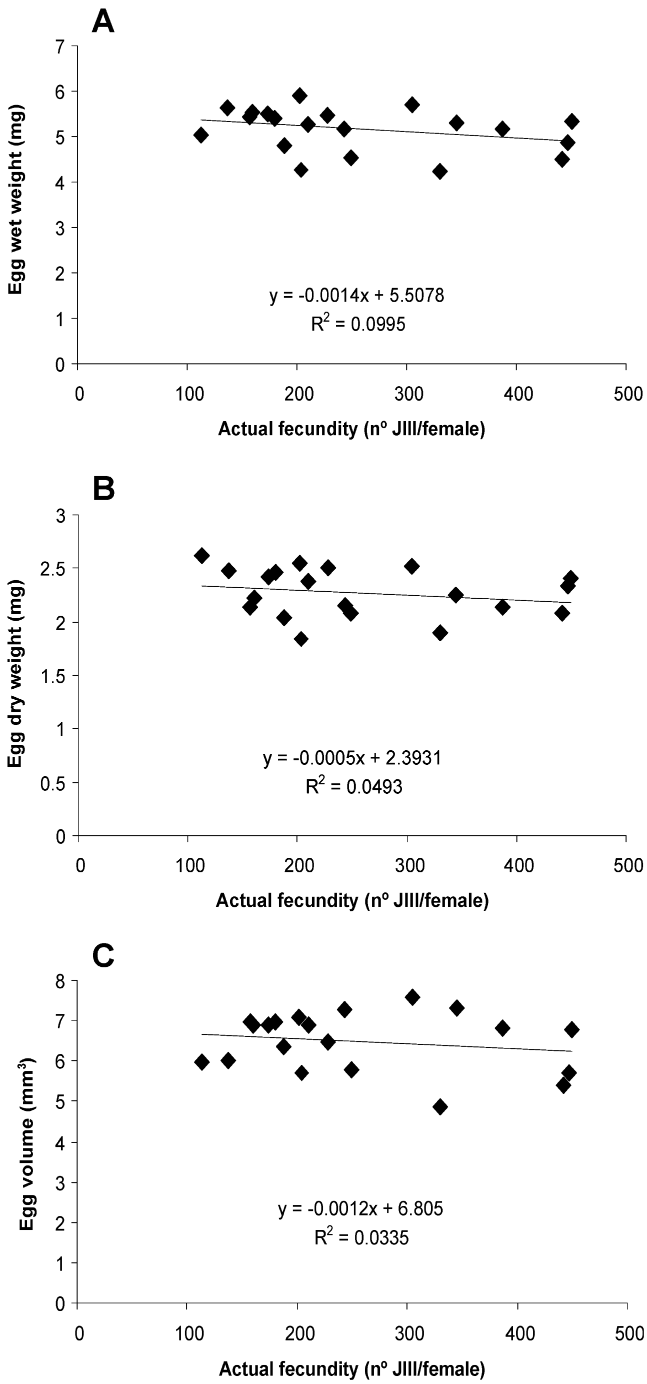

Fig. 2. Relationship between egg metrics and actual fecundity for the freshwater crayfish *Cherax quadricarinatus* (von Martens, 1868). A, egg wet weight; B, egg dry weight; C, egg volume (n = 20).

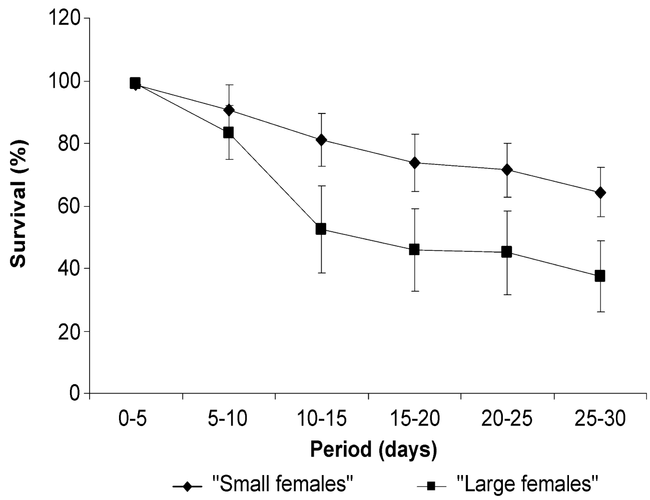

Fig. 3. Survival of juveniles III from different-sized females ("large females" and "small females") of *Cherax quadricarinatus* (von Martens, 1868) during a 30 day-period. Each point of the curves corresponds to the mean survival value of all the progenies from each treatment (10 for "large females" and 11 for "small females").

(Maguire et al., 2005), *Cambaroides japonicus* (De Haan, 1841) (Nakata and Goshima, 2004), *Pacifastacus leniusculus* (Dana, 1852) (Mason, 1978) and *Astacus leptodactylus* Eschscholtz, 1823 (Stucki, 1999), and in some anomuran and brachyuran species (van Dover and Williams, 1991; Fischer et al., 2009) the mean egg size/weight was demonstrated to increase with maternal size. Therefore, it seems that the relationship female size-egg size/weight is not associated to the type of postembryonic development (direct/indirect development).

The egg quality, on the other hand, is generally dependent on the spawner diets, since substantial quantities of protein and lipid that are synthesized from ingested food are required during ovarian maturation (Bromage, 1995; Harrison, 1997; García-Ulloa, 2000). In this sense, Rodríguez-González et al. (2006) found that the volume and weight of the eggs of *C. quadricarinatus* varied with the levels of crude protein in the diet of the spawners. In the present study, the fact that "small females" and "large females" were fed with the same diet may be a possible explanation for their similar egg quality.

Several authors documented in the American and European lobsters that egg size is closely linked to larval size, which implies that the former is a good approximation of the latter (Attard and Hudon, 1987; Hamasaki et al., 2003; Ouellet and Plante, 2004; Moland et al., 2010). Accordingly, the similarity observed in the present study in the volume and weight of eggs spawned by females of different weight resulted in a similar size and weight of the JIII. This may be explained by the type of post-embryonic development of *C. quadricarinatus*, in which juveniles go through an endogenous-feeding period after hatching (juveniles I and II), during which they depend on yolk reserves and remain attached to their mother. When they reach the juvenile stage III they get independent from their mother and begin to feed exogenously (Levi et al., 1999; García Guerrero et al., 2003). In the present study, JIII were sampled immediately after JII molting, in order to guarantee that these juveniles did not feed. Hence, the size of the JIII evaluated in this study would be determined at least in part by the yolk reserves transfer by the mother to the eggs.

These results show for the first time the absence of correlation between maternal weight and juvenile size in a decapod crustacean with direct development. All the studies performed in this field were in marine species with indirect development, and they show that, if there is a correlation between larvae/juveniles size and maternal size, it is generally positive (Jørstad et al., 2005; Moland et al., 2010; Sato and Suzuki, 2010).

Marshall et al. (2008) suggested that selection will act on both the mean and the variance of offspring size: "In an unpredictable environment where the range of viable offspring sizes is narrow, selection is likely to favor the production of variable offspring sizes. In contrast, when the environment is relatively stable and there is a broad range of viable offspring sizes, selection is likely to favor a constant offspring size within broods." The native environment of *C. quadricarinatus* fluctuates with a predictable seasonal pattern (Jones and Ruscoe, 2001; Lawrence and Jones, 2002; FAO, 2011), which would explain the low variance of offspring size found in the present study both within a brood and between different-sized females (see Table 1), according to the theory suggested by Marshall et al. (2008). However, the constant and controlled laboratory conditions could also be the reason for such homogeneity in juvenile size. A future study sampling from a wild population could potentially shed light on the possibility of differences being masked by this factor in captivity.

With regard to juvenile growth performance, no differences were detected between broods of "large females" and "small females." The survival of juveniles tended to be lower in broods from "large females," with the greatest mortality occurring from day 10 to day 15, a period that approximately coincides with the moment at which JIII molt to JIV (Stumpf et al., 2010). This result contributes to expand the scarce bibliography available at present about maternal influence on the performance of advanced larval/juvenile stages. The exposure of juveniles from different-sized females to stressful conditions would be of great interest to determine if maternal influence (given by female body weight) expresses solely, or stronger, when resource availability is restricted, as was proposed by Moland et al. (2010).

In summary, the results obtained in the present study show that although the AF was lower in "small females" in relation to "large females," the former allocated more energy to fecundity than the latter. The remaining production variables, together with the egg and JIII morphological/morphometrical parameters and juvenile growth, did not vary with female weight in the freshwater crayfish *C. quadricarinatus*. On this basis, we conclude that under controlled and constant laboratory conditions, the quality of the offspring of different-sized females is the same, with this outcome having a great importance both from a theoretical and an economical point of view.

Acknowledgements

The work reported in this paper is part of a postgraduate scholarship (CONICET) and PhD Thesis by Carolina Tropea (University of Buenos Aires, Argentina). Laura S. López Greco is grateful to Agencia Nacional de Promoción Científica y Tecnológica (PICT 2004, project 953, and PICT 2007, project 01187), CONICET (PIP 2009-2011, number 129) and UBACYT (projects X458 and 20020100100003) that funded this research.

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RECEIVED: 15 May 2012.
ACCEPTED: 25 July 2012.