

Egg production of the burrowing shrimp *Callichirus seilacheri* (Bott 1955) (Decapoda, Callianassidae) in northern Chile

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Received: 29 November 2007 / Revised: 6 May 2008 / Accepted: 30 June 2008 / Published online: 23 July 2008
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Abstract The thalassinidean shrimp *Callichirus seilacheri* is a common species in the intertidal zone of the South American Pacific coast. However, our knowledge of its reproductive ecology is rather limited. The present study was carried out between January and December 2003 at Las Machas, northern Chile. Although ovigerous females were encountered almost throughout the study period, they were particularly abundant between May and September when water temperatures were lowest and sediment coverage of the burrow entrances was highest. Females of *C. seilacheri* produced numerous ($17,450 \pm 3,796$ eggs) and small (0.884 ± 0.080 mm; 0.262 ± 0.054 mm³) eggs when compared to other thalassinidean shrimps for which such information is available. Fecundity was positively correlated with female size; however, correlations were allometric, which might be related to the elasticity of the abdomen. Egg volume increased by 41.2% during embryogenesis, and egg loss during the incubation period

was on average 8%. Females inverted on average 14.9% of their dry weight into egg production.

Keywords Fecundity · Reproductive output · Accretion · Callianassidae · Northern Chile · Egg loss

Introduction

The shrimps of the Infraorder Thalassinidea are considered as engineering organism due to their capacity to build complex networks of galleries below the surface (Berkenbusch and Rowden 2003). Their life cycle, except for the larval phase usually proceeds in cryptic habitats which may explain at least partially the lack of available information on the reproductive ecology of most of its representatives. During the last decade, our knowledge about several aspects of the life history of thalassinidean shrimps has increased significantly (e.g. Kevrekidis et al. 1997; Nates and Felder 1999; Berkenbusch and Rowden 2000; Bilodeau et al. 2005; Hernáez and Wehrtmann 2007). However, information especially on egg production and energy investment for reproduction remained limited.

Female size explains only part of the observed variability in the fecundity of thalassinidean shrimps; the correlation coefficient (r) reported for some species of this group (e.g. Hanekom and Erasmus 1989; Souza et al. 1998; Berkenbusch and Rowden 2000) is usually considerably lower than that observed in brachyuran and anomuran decapods (Hines 1991; Corey and Reid 1991; Reid and Corey 1991). It is assumed that the cryptic life may bring about an important egg loss while females move around in the galleries, thus explaining the relatively low correlation between female size and egg production (Thessalou and Kiortsis 1997).

Communicated by H.-D. Franke.

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Egg size is one of the most variable parameter in decapods and offers valuable information on a species' reproductive strategy. It is a useful indicator of the duration of embryogenesis and larval size at hatching (Steele and Steele 1975). Moreover, several studies on thalassinidean shrimps showed a clear relation between egg size and type of larval development (Forbes 1973; Felder and Griffis 1994; Thessalou et al. 1999). Such information, however, is restricted to just a few thalassinidean species.

The energy inverted in reproduction of decapods can be described as reproductive output (RO, Pianka 1972). Although this value varies among species and even within the same species (Wehrtmann and Kattner 1998), it is assumed that many female decapods devote around 10% of their body weight to the production of eggs (Hines 1982, 1991; Lardies and Wehrtmann 1996; Hernáez and Palma 2003; Brante et al. 2004). The RO is unknown for the majority of thalassinidean shrimps, particularly for those species inhabiting the southeast Pacific coast.

Considering thalassinidean shrimps of the Americas, representatives of the genus *Callichirus* Stimpson, 1866 are a common element of the intertidal and subtidal zone of some sandy beaches (Felder and Griffis 1994). Currently, this genus comprises three species; however, only *C. seilacheri* Bott 1955 (= *C. garthi*; Retamal 1975; see Sakai 1999) can be found along the eastern Pacific coast (12°N–37°S; Sakai 1999). Both the life cycle and the population dynamics of *C. seilacheri* seems to be strongly influenced by temperature and sediment movements (Hernáez and Wehrtmann 2007). Despite of the fact that this species is characteristic of many sandy beaches along the Chilean coast (Aste and Retamal 1983), its reproductive biology is completely unknown, a situation similar to that in most other thalassinideans of the Americas. The present study analyzed fecundity, egg characteristics, and RO of *C. seilacheri*. Additionally, we compiled and compared the published information about the reproduction of other thalassinideans which may facilitate a better comprehension of the reproductive strategies of these burrowing shrimps.

Methods

Study area

Shrimps were collected monthly from January to December 2003 in the intertidal zone of the beach Las Machas, northern Chile (18°25'S–70°19'W). This sector is characterized by fine sediments of terrigenous origin, supplied by the rivers Lluta and San José (Soto et al. 2002). The beach is wide open and influenced by high energy waves, especially during autumn (April–June) and winter (July–September). The physical structure of the beach shows a

seasonal pattern with the formation of wide intertidal plains during the summer, and an increased accretion during autumn and winter (Hernáez and Wehrtmann 2007). The presence of *C. seilacheri* is restricted to the area between the rivers Lluta and San José (approximately 8 km), with high gallery densities in the intertidal zone (P. Hernáez, pers. obs.).

Analyses of material

Specimens were collected with a yabby pump (diameter: 77 mm), and surface water temperature was measured to $\pm 0.1^\circ\text{C}$. Ovigerous females were put into individual plastic bags and transported to the laboratory of the Universidad Arturo Prat in Iquique, northern Chile. The following parameters were measured for each individual: total length (TL; ± 0.1 mm; from anterior carapace margin to posterior region of telson), carapace length (CL; ± 0.1 mm; from anterior to posterior carapace margin) and wet weight (± 0.1 g).

We detached the total egg mass from the ovigerous female and separated three subsamples of 100 eggs each, which were dried for 48 h at 65°C together with the remaining egg mass. Subsequently, each subsample and the remaining egg mass were weighed on an analytical balance (Sartorius; ± 0.1 mg). Egg weight and total egg number were calculated according to the following equations:

$$E = S/100 \quad (1)$$

$$NE = OM/E \quad (2)$$

with E = egg weight, S = average weight of subsample, NE = total egg number; OM = weight of total egg mass.

Developing eggs of *C. seilacheri* were classified into three stages (Stage I–III) considering shape and the development of both abdomen and eyes as described by Wehrtmann (1990). We separated arbitrarily 20 eggs from the egg mass and measured the width and length of each egg under a microscope equipped with a calibrated ocular micrometer. These data were used to calculate egg volume (EV) according to the formula proposed by Turner and Lawrence (1979) for oblate spheroids: $EV = 1/6 (a \times b^2 \times \pi)$, where a represents length, and b width.

The RO was estimated exclusively for females carrying recently produced eggs (Stage I), applying the formula proposed by Clarke et al. (1991):

$$RO = \frac{\text{dry weight of the entire egg mass}}{\text{dry weight of the female without eggs}}$$

Data analyses

The relation between fecundity and female size is described by an allometric model ($Y = aX^b$), which has been used widely for this purpose in similar studies on other

decapods (e.g. Hines 1991; Corey and Reid 1991; Hernandez and Palma 2003). According to Somers (1991), an isometric relation is indicated by values for b near to 3. Thus, b values of <2.90 and >3.10 were taken as indication of a negative and positive allometric relation, respectively (see Hernandez and Wehrtmann 2007). An analysis of covariance (ANCOVA; Zar 1999) was applied to the relation between egg number and CL for each embryonic stage to estimate egg loss during the incubation period. In case of a significant difference ($P < 0.05$), a Tukey a posteriori test was used to establish the similarity between each pair of developmental stages (Zar 1999).

Results

A total of 716 individuals of *C. seilacheri* were analyzed. Forty-eight of them revealed as ovigerous females (6.7%) with CL ranging from 18.6 to 23.2 mm (average 21.7 ± 0.83 mm). A majority of the ovigerous females (95%) measured between 20 and 23 mm CL.

The number of eggs carried by the females varied between 9,612 and 25,550 (average: $17,450 \pm 3,796$). The fecundity increased significantly with both female size and weight (Table 1). Correlation was relatively low, except for CL where the coefficient was almost 90% (Fig. 1). All relations tested to explain egg production in *C. seilacheri* tended to be allometric (Table 1). Considering exclusively females with eggs of Stages I and II, fecundity tended to be higher and egg volume to be smaller in the cold than in the warm period (fecundity, June–September: $18,278 \pm 3,905$ eggs; November–May: $16,718 \pm 4,775$ eggs; egg volume, June–September: 0.227 ± 0.031 mm³; November–May: 0.243 ± 0.017 mm³). However, differences in both fecundity and volume of egg were not statistically significant (t test, $P > 0.05$).

Table 1 Ovigerous females of *Callichirus seilacheri*

Equation	R	R^2	N
Fecundity versus size/wet weight			
1. $\log NE = 2.621 + 1.654 \log CL$	0.897	0.805	48*
2. $\log NE = 1.672 + 1.271 \log TL$	0.536	0.288	48*
3. $\log NE = 3.680 + 0.304 \log WW$	0.528	0.278	48*
Wet weight versus body size			
4. $\log WW = 0.893 + 1.974 \log CL$	0.618	0.382	48*
5. $\log WW = 0.145 + 3.269 \log TL$	0.796	0.634	48*

Allometric regression equations for the estimation of egg production R correlation coefficient, R^2 determination coefficient, N number of females analyzed, CL carapace length, NE number of eggs, TL total length, WW wet weight

* Statistically significant ($P > 0.05$)

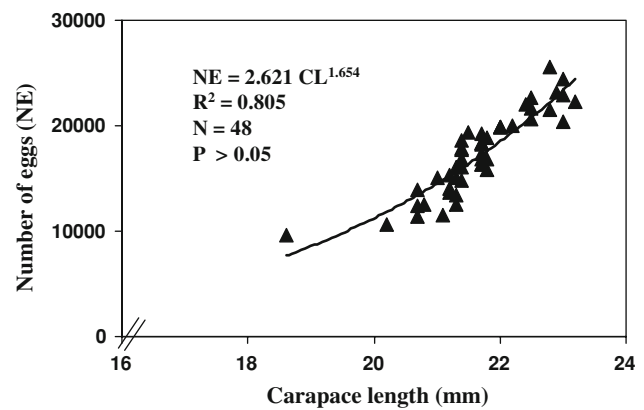


Fig. 1 Relation between carapace length (CL) and number of eggs (NE) of ovigerous females of *Callichirus seilacheri* from northern Chile

Ovigerous females were encountered almost throughout the study period, with the exception of January–February and October. The highest frequency of egg bearing females was observed from May to September, when mean water temperatures were lowest (Table 2). The vast majority of females with recently extruded eggs (Stage I: 92%) was collected between May and July, when water temperature started to decline (Table 2).

During the incubation period, females of *C. seilacheri* lose 8% of their initially produced eggs (ANCOVA, $f = 3.38$; $P < 0.05$). No statistically significant differences were detected between numbers of eggs carried by females with eggs in Stages I and II; however, females with eggs in Stage III carried significantly lower numbers of eggs than females with eggs in Stages I and II, respectively (Tukey test, $P < 0.05$). During embryogenesis, egg volume increased from 0.216 ± 0.021 SD ($N = 12$) to 0.305 ± 0.054 SD mm³ ($N = 20$), representing an overall increment of 41.2%. Egg length ranged between 0.765 and 1.213 mm (average: 0.887 ± 0.078 mm). Females inverted on average $14.90 \pm 3.88\%$ of their dry weight into egg production, and RO varied between 8.3 and 22.4%. No statistically significant differences were detected for RO values among months (ANOVA, $f = 0.05$, $P > 0.05$).

Discussion

Information on the reproductive biology of ghost shrimps generally refers to relatively small sample sizes, and the reported percentage of ovigerous females ranged between 4 and 35% of all collected individuals (Kevrekidis et al. 1997; Nates and Felder 1999; Berkenbusch and Rowden 2000). Thus, both our sample size (716 individuals) and the percentage of egg carrying females (6.7%) are in the range of previously published studies on thalassinidean shrimps.

Table 2 Ovigerous females of *Callichirus seilacheri*

Month	Number of ind.	Carapace length (mm)	Egg number	Egg length (mm)	Seawater temperature (°C)	Sediment coverage of burrows ^a
January	–	–	–	–	18.6 ± 1.66	–
February	–	–	–	–	20.2 ± 0.72	–
March	1	22.0 ± 0.0	19,846 ± 0.0	1.213 ± 0.0 ^b	18.0 ± 0.85	–
April	2	20.2 ± 1.10	13,955 ± 6,141.9	0.731 ± 0.032	17.7 ± 1.52	–
May	9	21.4 ± 0.07	15,953 ± 3,970.5	0.756 ± 0.045	17.1 ± 0.77	X
June	11	21.4 ± 0.07	16,347 ± 3,240.5	0.735 ± 0.041	16.2 ± 1.69	X
July	7	22.2 ± 0.11	20,585 ± 4,573.8	0.713 ± 0.033	15.9 ± 0.98	X
August	9	21.9 ± 0.07	18,002 ± 2,656.3	0.775 ± 0.027	16.1 ± 1.78	X
September	5	22.0 ± 0.15	18,394 ± 2,773.9	0.736 ± 0.048	15.8 ± 0.54	–
October	–	–	–	–	17.3 ± 1.44	–
November	2	21.9 ± 0.46	18,347 ± 6,130.6	0.744 ± 0.032	17.3 ± 1.37	–
December	2	21.5 ± 0.14	15,833 ± 3,436.5	0.783 ± 0.038	17.1 ± 1.49	–
Total	48	21.6 ± 0.83	17,450 ± 3,796.8	0.749 ± 0.044	17.3 ± 1.27	
<i>F</i> (test value)		1.91	1.35	6.90		
Probability		>0.05	>0.05	<0.001	<0.05	

Monthly variation of number of collected egg-bearing females, carapace length, number and length of eggs (independent of embryonic development), seawater temperature, and sediment coverage of burrows during of the study period (January–December 2003)

X covered; – not covered

^a According to Hernáez and Wehrmann (2007)

^b Eggs in Stage III

According to Coelho et al. (2000), the relatively low number of individuals reported in demographic studies of ghost shrimps might be due to the cryptic life style of these species. It might be speculated that egg-bearing females are situated deeper in the sediment and, thus, not easily accessible to the yabby pump. Another explanation might be related to the polygamist behavior of the species (Hernáez and Wehrmann 2007), assuming that a male fertilizes only one or a limited number of females of his harem. However, the present contribution was not designed to test these assumptions, and further studies are required to

explain the low frequency of ovigerous females in *C. seilacheri* and other thalassinidean shrimps.

The considerable variability among thalassinidean species in fecundity and egg size (Table 3) may indicate important differences in the reproductive strategy, and may also reflect a latitudinal trend as observed in other decapods (Thorson 1950; Sastry 1983; Clarke 1987, 1992; Brante et al. 2004). *C. seilacheri* produces the highest number of eggs compared to those thalassinideans where data are available. However, this thalassinidean shrimp is the largest species among those listed in Table 3, and it is assumed

Table 3 Carapace length of ovigerous females, and number and length of eggs in some thalassinidean shrimps

Species	Carapace length (mm)	Number of eggs	Egg length (mm)	References
<i>Callinassa filholi</i>	5.5–14.9	1,985	0.68	Berkenbusch and Rowden (2000)
<i>C. kraussi</i>	n.a.	122	1.52	Forbes (1973)
<i>C. tyrrhena</i>	5.2–10.4 ^a	270	1.18	Thessalou (1987)
<i>Callichirus major</i>	n.a.	8,170	0.88	Pohl (1946)
<i>C. seilacheri</i>	18.6–23.2	17,450	0.88	Present study
<i>Lepidophthalmus louisianensis</i>	n.a.	598	n.a.	Nates et al. (1997)
<i>L. sinuensis</i>	7.0–16.8	251	1.22	Nates and Felder (1999)
<i>Upogebia affinis</i>	n.a.	10,000	n.a.	Pearse (1945)
<i>U. deltaura</i>	16.6–18.9	4,757	0.56	Tunberg (1986)
<i>U. pusilla</i>	14.7–16.6	n.a.	n.a.	Kevrekidis et al. (1997)

n.a. information not available

^a Obtained from regression equation

that the area available for egg attachment increases with female size (Hines 1982; Corey and Reid 1991). When compared to a similar-sized species (*Upogebia deltaura*: 18.9 mm CL, 5,304 eggs; Tunberg 1986), fecundity in *C. seilacheri* is still substantially higher (18.6 mm CL, 9,612 eggs); moreover, *C. seilacheri* produces considerably larger eggs than *U. deltaura* (0.884 and 0.558 mm, respectively). It is speculated that these differences in egg numbers in similar-sized species are related to the elasticity of the abdomen in *C. seilacheri* (Manning and Felder 1991), which provides more space for egg attachment.

Fecundity in *C. seilacheri* was strongly correlated with carapace length (Table 1). The correlation coefficient (0.89) was substantially higher than those reported for other thalassinidean shrimps (0.55–0.77; Hanekom and Erasmus 1989; Souza et al. 1998; Berkenbusch and Rowden 2000). However, egg production in *C. seilacheri* increased allometrically in relation to both female size and weight, which indicates a disproportion among the variables associated with this relation (Somers 1991). This might be related to the different dimensions used for the description of fecundity (volumetric) and female size (linear) (see Somers 1991). We assume that the elasticity of the abdomen of *C. seilacheri* (as described for other ghost shrimps; Manning and Felder 1991) leads to an overestimation of TL, which in turn results in a disproportion of the different biometrical parameters measured (allometry). This interpretation is supported by the observation of Felder and Lovett (1989) who attributed the observed allometric increase between gonad weight and female size of *Lepidophthalmus lousianensis* to the elasticity of the abdomen.

Egg length of *C. seilacheri* is relatively low when compared to other thalassinidean species (Table 3). It has been demonstrated that egg size is correlated with both the duration of embryogenesis and the size of hatchlings (Steele and Steele 1975; Wehrmann and López 2003). Regarding thalassinideans, the available information demonstrate that species with an abbreviated larval development such as *Callinassa kraussi* (Forbes 1973), *C. tyrrhena* (Thessalou et al. 1999) and *L. sinuensis* (Nates et al. 1997) produce larger eggs than those with extended larval development (*C. filholi*: 0.68 mm, Berkenbusch and Rowden 2000). According to Aste and Retamal (1983), the larval development of *C. seilacheri* consists of five larval stages; thus our egg volume data confirm that relatively small eggs indicate a prolonged larval period.

Egg loss in *C. seilacheri* was insignificant when compared to the thalassinidean shrimp *Calocaris macandreae* (66%; Buchanan 1963) and other decapods (for review, see Kuris 1991). During embryogenesis, *C. seilacheri* lost 8.6% of the initially produced eggs, while the egg volume increased by more than 40%. In accordance with other

studies on egg production in decapods (Kuris 1991), it is assumed that—due to limited space for attachment—the swelling of the eggs during embryogenesis results in a reduction of the number of incubated eggs.

Females of *C. seilacheri* inverted 14.9% of their body weight into the production of eggs. This value is slightly lower than that reported for *C. tyrrhena* (19.6%, Thessalou and Kiortsis 1997), but in the range of RO values (3–22%) described for brachyuran crabs (Hines 1991; Brante et al. 2004) and higher than those published for anomurans (3–10%; Lardies and Wehrmann 1996; Hernáez and Palma 2003). Additional RO data for thalassinidean shrimps are needed to test whether the species' cryptic life may allow for a higher energy allocation to reproduction.

The reproductive cycle of many decapods, especially of those in temperate and cold-water zones, is synchronized with the temporal variation of environmental factors such as temperature, photoperiod, and food availability (Clarke 1987; Bauer 1992; Kevrekidis et al. 1997; Berkenbusch and Rowden 2000; Lardies et al. 2004). In our study the number of collected ovigerous females increased with decreasing temperatures, which coincided with the period when the burrow entrances of *C. seilacheri* were usually covered by a sediment layer. However, the mechanism of providing sufficient oxygen for the embryos inside the covered burrow remains to be studied.

Acknowledgments The first author (PH) is grateful to the Universidad Arturo Prat, Iquique, Chile, especially the Museo del Mar, for providing facilities to analyze the collected material. We greatly appreciate the critical comments by Fresia Villalobos and Yurlandy Gutierrez on an earlier draft of the manuscript, which helped to improve the manuscript.

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