

Reproductive strategy of the shrimp *Nematopalaemon schmitti* (Decapoda, Caridea, Palaemonoidea) on the southeastern coast of Brazil

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ABSTRACT

The goal of this study was to evaluate the reproductive investment (RI) and the fecundity of the shrimp *Nematopalaemon schmitti* (Holthuis, 1950), caught by trawling in the southeastern Brazilian coast in 2008, 2009 and 2011. The carapace length (CL) of ovigerous females was measured and the development stage of their ovaries and embryos were analyzed. A significant

relationship was observed between the female body and embryo weights (Linear regression: $r^2 = 0.26$, $F = 20.77$, $P < 0.0001$, $\text{Ln BDW} = 0.92$, $\text{Ln FBDW} - 2.24$) and between number of embryos and CL (Linear regression; stage I: $r^2 = 0.38$, $F = 36.15$, $P < 0.0001$; stage II: $r^2 = 0.34$, $F = 14.10$, $P < 0.001$), but not between the RI and CL (ANOVA: $F = 0.47$, $df = 7$, $P = 0.85$). Association of the changes in embryo development and ovarian maturation of ovigerous females was tested. Females with rudimentary ovaries predominantly showed embryos in stage I (early development) and females with developed ovaries only showed embryos in stage II (final development), showing synchrony between the development of both, thus supporting the hypothesis of a continuous reproductive cycle for *N. schmitti* in the region. Such information is fundamental for understanding the reproductive biology of these crustaceans, as well as other caridean shrimps, in order to promote the maintenance and preservation of natural stocks.

KEY WORDS

Crustacea, fecundity, ovary development, reproductive investment, Western Atlantic.

INTRODUCTION

Reproductive characteristics of crustaceans may vary according to intrinsic individual aspects such as the size and age of females, as much as environmental conditions (Sastry, 1983). This can reflect adaptive mechanisms of a species, such as influencing the number and size of embryos and the reproductive investment of individuals. All these reproductive features play an important role in the biology and ecology of the species (Yoshino *et al.*, 2002). Changes in volume of crustacean embryos were verified by Sastry (1983) in latitudinal, depth, thermal and salinity gradients, while significant differences in reproductive investment of freshwater and marine caridean shrimps were tested by Anger and Moreira (1998). This evidence shows that analysis of newly fertilized embryos might indicate responses to selective pressures, which might affect the reproductive investment and larval development of crustaceans (Bauer, 1991).

Studies on the reproduction of caridean shrimps have pointed to reproductive investment (RI) and fecundity (F) as important and quantifiable measures of the species' reproductive effort (e.g., Clarke *et al.*, 1991; Clarke, 1993; Anger and Moreira, 1998; Wehrmann and Lardies, 1999; Kim and Hong, 2004; Oh and Hartnoll, 2004; Chilari *et al.*, 2005; Pavanelli *et al.*, 2008; Echeverría-Sáenz and Wehrmann, 2011). The division between the dry weight of the brood and dry weight of the female defines RI (Hines, 1982). Fecundity is the number of embryos released by a female during a single spawning event or specific period

of its life history (Negreiros-Fransozo *et al.*, 1992; Ramírez-Llodra, 2002). In general, both RI and F show a strong relationship with some body dimensions of the species, and its respective variations in spatial and temporal scales.

Despite not being marketed, the population of whitebelly shrimp *Nematopalaemon schmitti* (Holthuis, 1950) is a bycatch under heavy impact due to fishing activity conducted directly towards species of commercial interest on the southeastern coast of Brazil (Almeida *et al.*, 2012). Such activity can cause imbalance in the marine trophic web community to which *N. schmitti* belongs. This caridean shrimp has ecological importance in the habitat, serving as a food source for other invertebrates and fish (Fransozo *et al.*, 2009; Almeida *et al.*, 2012). Nevertheless, publications related to this species are restricted to spatial and temporal variations in abundance and associated with abiotic factors (Fransozo *et al.*, 2009; Almeida *et al.*, 2012), its population structure and reproductive period (Almeida *et al.*, 2011). These publications show that *N. schmitti* inhabit temperatures around 23°C (usually recorded during autumn and winter), in areas where the sediment is composed of fine and very fine sand, silt and clay, and in the presence of algae and plant fragments (Fransozo *et al.*, 2009; Almeida *et al.*, 2012). Concerning the population structure of the whitebelly shrimp, there is a difference in body size, with males attaining smaller sizes than females. In addition, *N. schmitti* shows a continuous reproduction pattern along the northern coast of São Paulo State (Almeida *et al.*, 2011).

Considering the importance of the reproductive features of natural shrimp populations, this study focused on two aspects of the reproduction of *N. schmitti*, namely its RI and F. Furthermore, association between ovarian maturation and embryo development were tested for a better understanding of the species life cycle in order to promote the maintenance and preservation of natural stocks.

MATERIAL AND METHODS

Shrimp samples were collected from Ubatuba Bay (23°30'S 45°09'W), São Paulo, during November 2008, January 2009 and July 2011 using a fishing boat carrying double-rig nets (4.5 m wide; 20 mm and 15 mm mesh diameter on the body and cod end of the net, respectively).

Females carrying embryos at different development stages were immediately stored individually in glass vials, placed in an ice chest filled with ice, transported to the laboratory and stored frozen until analysis. Females were then measured and their embryos and ovarian development were examined. The carapace length (CL, the distance from the orbital angle to the posterior margin of the carapace) of each female was measured with a Mitutoyo caliper (precision = 0.1 mm). After that, each female was examined under a Zeiss stereomicroscope (Stemi SV6 model) to record the embryonic stage and ovarian development. Despite embryonic development being classified in up to four stages, we only collected females with embryos in two stages of development: (1) embryos just spawned with no visible eyes, no visible blastoderm and uniformly distributed yolk and (2) embryos near hatching with large developed eyes and no yolk (modified from Corey, 1981; Jewett *et al.*, 1985). Three ovarian development stages were recognized, taking into account the color and volume of the ovary (modified from Bauer and Abdalla, 2000). They were characterized as follows: 1) rudimentary ovaries filling less than half of the space in the cephalothorax, having a translucent white coloration; 2) developing ovaries with light orange coloration filling most of space in the cephalothorax; and 3) developed ovaries (near spawning) with dark orange coloration filling all the space in the cephalothorax and the first abdominal segment.

All embryos attached to the pleopods of each female were carefully removed using dissecting

needles and a fine brush and then counted under the stereomicroscope. Each female and their embryo mass were dried for 48 h at 60°C in a Lufanco stove (41179 model) and then weighed with a Marte analytical balance (precision = 0.001 g; AL 500 C model). The embryo number of females with stage 1 or 2 was compared by means and Student's t-test.

RI and F were analyzed based on weight and body size measurements, respectively. In addition, the brood production of the whitebelly shrimp was characterized according to changes in the ovarian maturation and embryo development. RI (RI = brood dry weight / female body dry weight – Clarke *et al.*, 1991) was analyzed based on females carrying initial embryos (Stage I), to avoid embryo loss effect.

Differences in the RI were analyzed by size classes in an interval of 0.5 mm CL using analysis of variance (One-way ANOVA, $\alpha = 0.05$), followed by a multiple comparison test (Tukey, $\alpha = 0.05$). Fecundity of each female was obtained from both stages 1 and 2 of embryonic development. The relationships between brood dry weight (BDW) and female body dry weight (FBDW), and F and CL were examined using the best fit model, which in this case was the power function $y = ax^b$, converted to the linear form, $\ln y = \ln a + b \ln x$, by means of natural logarithm transformation (y = dependent variables [F or BDW]; x = independent variable [CL or FBDW]; a = y-intercept; and b = slope). The slope (b) of the ln-ln least squares regression represents the rate of exponential change of each reproductive parameter with an increase in CL or body weight of female shrimps. When $b > 3$ or $b < 3$, F increases or decreases linearly. In turn, when $b > 1$ or $b < 1$, brood dry weight increases or decreases linearly. When $b = 3$ or $b = 1$, no linear increase or decrease of the slopes are observed for the relationships between F and CL, or between brood dry weight and female body dry weight, respectively. Statistically significant departures from these coefficients were tested using the Student's t-test (Zar, 2010).

We estimated embryo loss (%) – difference between the embryo numbers in stage 1 and 2 – during embryonic development. The hypothesis of no embryo loss during development was tested using the Student's t-test (Zar, 2010). In this test, embryo stage (I vs. II) was used as the factor to estimate differences between females carrying embryos in different stages of development.

Lastly, the hypothesis of successive spawning was examined as in Bauer and Newman (2004) and Baeza (2006) by determining the association between embryonic and ovarian development. For this purpose, the association between embryonic and ovarian development categories was tested with the Goodman's test, which analyzes the contrasts between and within multinomial proportions (Goodman, 1965; Curi and Moraes, 1981). In this case, if females spawn successively after every molt, then the degree of embryonic development should be positively correlated with the degree of ovarian development.

Tests for homoscedasticity and normality of the contrasted data sets (after ln-ln transformation) were examined for all analyses above and found to be satisfactory (Zar, 2010).

RESULTS

We analyzed 90 females carrying embryos at different stages of development. Carapace length of ovigerous females varied from 10.2 to 13.7 mm, with mean (\pm standard deviation) of 11.6 ± 0.7 mm (Tab. 1).

Differences among RI and size classes were not statistically detected (ANOVA: $F = 0.47$, $df = 7$, $p = 0.85$), while the relationship between female weight and the embryo mass weight was positively statistically significant (Linear regression: $r^2 = 0.26$, $F = 20.77$, $P < 0.0001$, $\ln \text{BDW} = 0.92$, $\ln \text{FBDW} - 2.24$), with an isometric relation to brood dry weight and female body dry weight. There was no statistically significant association between RI and CL (ANOVA: $F = 0.47$,

$df = 7$, $P = 0.85$). The average RI was $12.4\% \pm 4.1\%$, ranging from 5.5% to 24.8%. Total estimated RI was 12.41% (Fig. 1).

Fecundity of females carrying initial (stage I – $N = 61$) and final (stage II – $N = 29$) embryos varied between 901 and 3,293 embryos ($1,587.47 \pm 496.78$ embryos) and between 708 and 2,310 embryos ($1,422.79 \pm 386.26$ embryos), respectively. There was a loss of 10% of embryos during development, but no statistical difference was observed between the number of embryos at different stages of development (Student's t-test, $p = 0.14$), with an isometric relation to F and CL ratio. A statistically positive association between F and CL was detected for females carrying both initial and final stage embryos (Linear regression; stage I: $r^2 = 0.38$, $F = 36.15$, $P < 0.0001$, $\ln \text{NE I} = 2.97$, $\ln \text{CL} + 0.03$; stage II: $r^2 = 0.34$, $F = 14.10$, $P < 0.001$, $\ln \text{NE II} = 2.57$, $\ln \text{CL} + 0.97$) (Fig. 2).

Lastly, the association between ovarian and embryonic development was statistically significant (Goodman's test, $P < 0.05$). It is possible to observe changes in the embryonic development associated to the ovarian maturation of females analyzed in the present study (Fig. 3). Considering the developmental stages of embryos, there was a predominance of females with embryos in stage I (67.80%), followed by stage II (32.20%). In relation to gonadal development, it was observed that most females had rudimentary ovaries (53.33%), while females with developing and developed ovaries accounted for 34.44% and 12.22% of the total abundance, respectively. Females with

Table 1. *Nematopalaemon schmitti* (Holthuis, 1950). Number of ovigerous females by size class, gonadal development stage (Rudimentary, Developing, Developed), and embryo development stage (I) and (II). CL = carapace length (mm); I = initial embryonic development; II = final embryonic development.

Gonad Stage		Rudimentary		Developing		Developed		Total
Embryonic stage		I	II	I	II	I	II	
Size Classes	CL (mm)							
1	10.0 -- 10.5	1	0	1	2	0	1	5
2	10.5 -- 11.0	7	1	3	2	0	1	14
3	11.0 -- 11.5	9	2	2	2	0	3	18
4	11.5 -- 12.0	17	2	3	2	0	4	28
5	12.0 -- 12.5	5	0	5	3	0	2	15
6	12.5 -- 13.0	2	0	2	2	0	0	6
7	13.0 -- 13.5	1	0	2	0	0	0	3
8	13.5 -- 14.0	1	0	0	0	0	0	1
Total		43	5	18	13	0	11	90

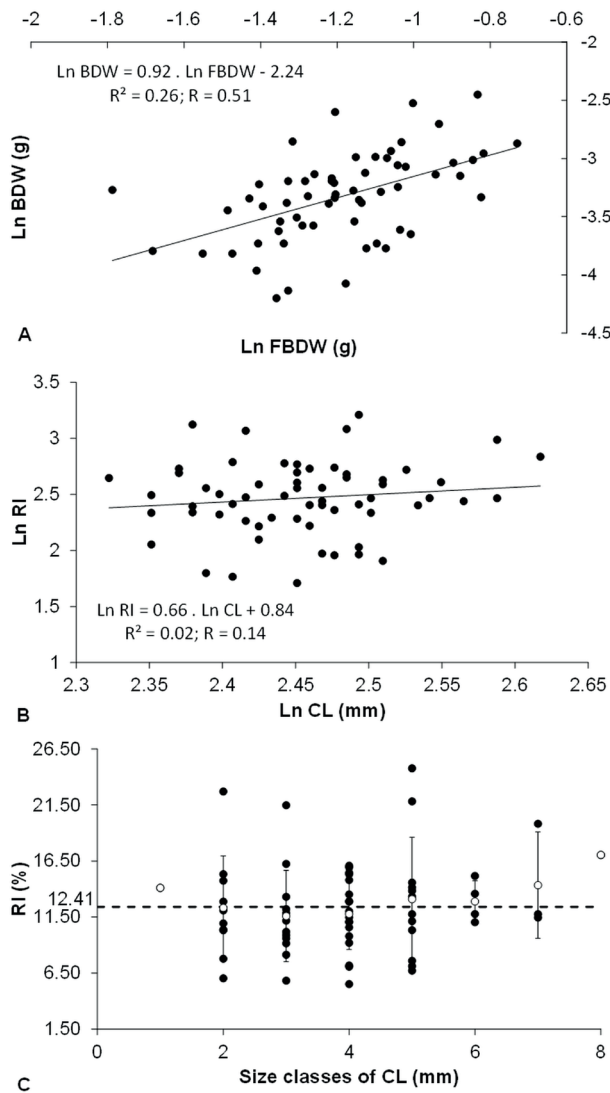


Figure 1. *Nematopalaemon schmitti* (Holthuis, 1950). Reproductive investment (RI) by: A) female body dry weight (FBDW) and brood dry weight (BDW) (g); B) carapace length (CL) (mm); C) size classes of carapace length (mm).

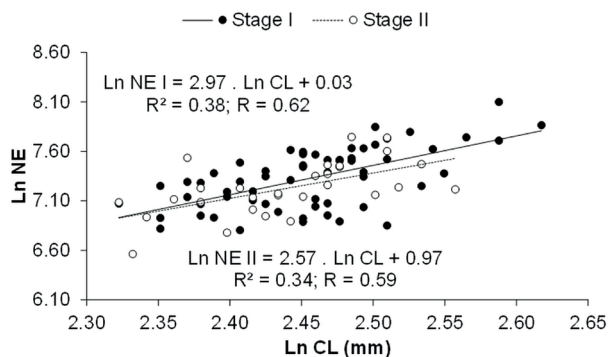


Figure 2. *Nematopalaemon schmitti* (Holthuis, 1950). Best fit model between ln number of embryos (NE) and ln carapace length (CL) (I = initial embryonic development, II = final embryonic development).

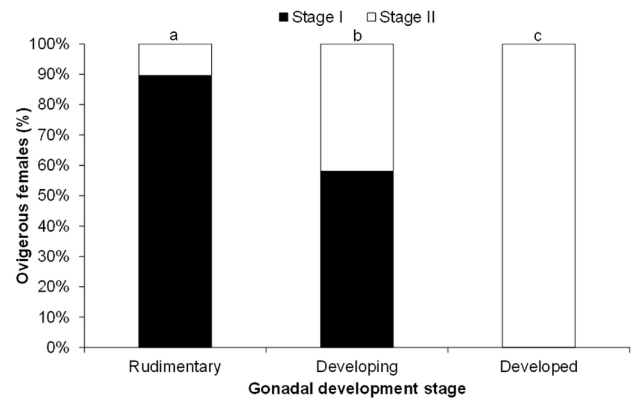


Figure 3. *Nematopalaemon schmitti* (Holthuis, 1950). Frequency of ovigerous females (N = 100) in each embryo development stage (I = initial, II = final) related to each gonadal development stage (Rudimentary, Developing, Developed).

rudimentary ovaries predominantly exhibited embryos at stage I, and females with developed ovaries only showed embryos in stage II (Fig. 3). However, females with developing ovaries showed embryos in both stage I and II (Fig. 3).

DISCUSSION

We observed a significant relationship between F and CL, and also between brood dry weight and female body dry weight. However, no association was observed between mean RI and CL, showing that females of all sizes make the maximum RI that they are capable. In general, the relationship between the RI and the CL can be influenced by different factors. With increasing latitude, for instance, there is a tendency of increasing embryo volume and decreasing embryo number (Clarke et al., 1991; Echeverría-Sáenz and Wehrtmann, 2011), as observed for *Pandalus borealis* Krøyer, 1838 at different latitudes between 79°10'N 10°40'E and 58°47'N 10°55'E (Clarke et al., 1991). In our study, which was in the Subtropical region (23°26'S to 45°02'W), the females seemed to allocate all their energy to embryo production, since environmental conditions, i.e. temperature and food availability, are more favorable. However, it is important to highlight the need for more studies at different latitudes to allow comparisons between the size and RI of *N. schmitti* associated with the latitudinal effect.

Assuming that female size is closely linked to reproductive strategies (Hines, 1982), the positive relationship between CL and number of embryos

observed in *N. schmitti* is corroborated by previous studies of other caridean shrimps, such as *Pandalus borealis* (Clarke *et al.*, 1991), *Hippolyte zostericola* (S. I. Smith, 1873) (Negreiros-Fransozo *et al.*, 1996), *Austropandalus grayi* (Cunningham, 1871) (Wehrtmann and Lardies, 1999), *Exhippolysmata oplophoroides* (Holthuis, 1948) (Chacur and Negreiros-Fransozo, 1999), *Hippolyte obliquimanus* Dana, 1852 (Mantelatto *et al.*, 1999) and *Palaemon gravieri* (Yu, 1930) (Kim and Hong, 2004). This positive relationship suggests that larger females produce more embryos because they have more energy resources and the ability to use it (Baeza, 2006), as well as more space in the abdomen to accommodate them (Clarke, 1993; Chacur and Negreiros-Fransozo, 1999; Mantelatto *et al.*, 1999). In this study, we also observed that smaller females produce fewer embryos than larger females. According to Calado and Dinis (2007), after the puberty molt of *Lysmata seticaudata* (Risso, 1816), the individual growth rate decreases and the energy resources are allocated to gonad maturation. In this sense, larger females have more energy resources available, as well as a larger abdomen to accommodate the embryos. Although RI does not vary significantly between size classes, larger females make a greater contribution to the RI of the population.

Although it is clear that the number of embryos is higher in larger females, the RI did not correlate with the CL, even analyzing the variation of such RI between the different size classes obtained for *N. schmitti*. Interestingly, even with a high RI variation, the average RI within each size class was generally close to the overall RI average, demonstrating that the RI can be an intrinsic characteristic of each female. Studies show that the number of embryos decreases with latitude, not only due to female size (Clarke *et al.*, 1991; Wehrtmann and Lardies, 1999), but also to the fact that some high latitude species have large embryos which hatch as lecithotrophic larvae with abbreviated development. However, F can vary with the number of consecutive spawns in the same reproductive cycle (Sainte-Marie, 1993), and due to loss of embryos during embryonic development (Mantelatto *et al.*, 1999). The embryo loss that occurs during development has been observed by many authors (Corey and Reid, 1991; Wehrtmann and Lardies, 1999; Nazari *et al.*, 2003; Kim and Hong, 2004; Oh and Hartnoll, 2004; Echeverría-Sáenz and

Wehrtmann, 2011), who have reported that such loss might occur during specimen sampling (depending on the methods used), or due to the increased embryo volume interferes with their accommodation in the abdomen, and also due to parasites and mechanical stress. Our results indicated that embryo loss may be occurring, but perhaps our sample size was not sufficient to adequately test this hypothesis.

In the study of Wehrtmann and Lardies (1999) with the caridean *A. grayi*, the females lost on average 51.1% of their initially-laid embryos. The authors related such loss to the sampling method, and also to embryo abrasion. For the caridean *Heterocarpus vicarius* Faxon, 1893, a loss of 46.9% was observed (Echeverría-Sáenz and Wehrtmann, 2011) and associated to the end of embryonic development, when the incorporation of a large quantity of water occurs in order to facilitate the larvae hatching. During this process, the embryos become larger and the space between them decreases, increasing abrasion and the consequent loss to the environment. Compared to other species, a lower embryo loss of 10% was observed for *N. schmitti*, which was similar to another caridean, *Exopalaemon modestus* (C. Heller, 1862) (Oh *et al.*, 2002), with a loss of around 7%. However, *E. modestus* inhabits a freshwater environment and is subject to different temperature and salinity compared to marine species. Moreover, the sampling method could have influenced this estimate, depending on the time and type of net used. The authors used a hand net for *E. modestus*, while trawling nets were used for *N. schmitti*. It is believed that trawling is more stressful for the animals, since they require longer sampling time.

By comparing the abundance of females according to each development stage of embryos and ovaries in the present study, it was possible to observe synchrony between the embryo and ovary development. In general, females with rudimentary ovaries had embryos in stage I, and females with developed ovaries only had embryos in stage II. According to these results, along with the continuous reproduction pattern of *N. schmitti* in the study region (Almeida *et al.*, 2011), it is assumed that the female reproductive cycle occurs as follows: females with ovaries in advanced development stage molt, copulate and then extrude their eggs which might or might not be fertilized. Later, the ovaries of these females become rudimentary while the embryos are

in the early development stages. During incubation, both embryos and ovaries almost develop in synchrony. When the larvae hatch, the ovaries are in an advanced stage of development, and the reproductive cycle continues. With these results, we argue in support of the hypothesis of successive spawning, as in Bauer and Newman (2004) and Baeza (2006).

In this study, we noted that the number of embryos extruded by *N. schmitti* is correlated to CL, showing that larger specimens have larger space available to accommodate the embryos in the abdomen and greater potential of energy resources for embryo production. Although larger females have more embryos, the RI was not significantly associated to female size. Through the wide geographic distribution of *N. schmitti* in the western Atlantic (Venezuela to Brazil) (Holthuis, 1980), studies that address the RI and F are critical for a better understanding of the reproductive biology of this species. The synchrony observed between the embryo and ovary development supports the standard cycle of continuous reproduction of *N. schmitti* in the study region. These results give us a better understanding, not only of the reproductive biology of this species, but also of other carideans which inhabit this region. In this sense, research of this nature is essential to propose effective conservation strategies such as impact mitigation on natural communities and important suggestions for conservation, and also provides support for new research that addresses the biology and ecology of decapod crustaceans.

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