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Research Article

Reproductive aspects of the caridean shrimp *Atya scabra* (Leach, 1815) (Decapoda: Atyidae) in São Sebastião Island, southwestern Atlantic, Brazil

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ABSTRACT. The caridean freshwater shrimp *Atya scabra* is a common resident of stream systems of tropical rainforests in America, including Brazilian drainages. This shrimp has an amphidromous life cycle, which increases its vulnerability when facing habitat fragmentation. Since information on the reproduction of this species is still limited, we present here data on egg production, egg loss, and energy investment, to achieve a better understanding of reproductive features of *A. scabra*. Specimens were collected between 2006 and 2007 in São Sebastião Island, southeastern Brazil, in 13 locations. The fecundity of 21 ovigerous females analyzed ranged between 414 and 19,250 eggs, which were higher than previously reported. However, the larger size of females analyzed may explain the observed intraspecific difference in egg production. During embryogenesis, egg volume and water content increased by 103 and 22.6%, respectively. The initial egg volume of *A. scabra* in the present study (0.027 mm³) was slightly lower, but comparable to the values reported previously from the same study area. During incubation, females of *A. scabra* lost 15% of their initially produced eggs. The reproductive output (average RO of 3.6%) is the first report for any atyid species. Its value is fairly low compared to other freshwater shrimps, and it is hypothesized that this might be related to a high energy investment in morphological adaptations, which allows the shrimp to cling on to the substrate in the fast flowing environment they inhabit. Additionally, the long life span, a well-known phenomenon in atyid shrimp, may allow the species to invest a relatively low amount of energy per brood in egg production, but over a longer time span.

Keywords: amphidromy, fecundity, neotropical, reproductive output, southwestern Atlantic, Brazil.

Aspectos reproductivos del camarón carideo *Atya scabra* (Leach, 1815) (Decapoda: Atyidae) en la isla de São Sebastião, Atlántico sudoccidental, Brasil

RESUMEN. El camarón carideo de agua dulce, *Atya scabra*, es un residente común del sistema de arroyos de los bosques tropicales de América, incluyendo drenajes brasileños. Este camarón tiene un ciclo de vida anfídromo, lo que aumenta su vulnerabilidad al enfrentar la fragmentación del hábitat. Dado que la información sobre la reproducción de esta especie es todavía limitada, se presentan datos sobre producción de huevos, pérdida de huevos e inversión energética, para lograr una mejor comprensión de los aspectos reproductivos de *A. scabra*. Los especímenes fueron recolectados entre 2006 y 2007 en la isla São Sebastião, al sureste de Brasil, en 13 localidades. La fecundidad de las 21 hembras ovígeras analizadas varió entre 414 y 19,250 huevos, valores que son más altos que los reportados previamente, sin embargo, el mayor tamaño de las hembras analizadas podría explicar la diferencia intraespecífica en la producción de huevos. Durante la embriogénesis, el volumen del huevo y el contenido de agua aumentó en 103 y 22,6%, respectivamente. El volumen inicial del huevo de *A. scabra* en este estudio (0,027 mm³), fue ligeramente inferior, pero comparable con los valores reportados anteriormente para la misma área de estudio. Durante el periodo de incubación, las hembras de *A. scabra* pierden el 15% de los huevos producidos inicialmente. El rendimiento reproductivo (RO promedio de 3,6%), es el primer valor reportado para cualquiera de las especies de la familia Atyidae. Este

valor, es relativamente bajo en comparación con otros camarones de agua dulce, y se plantea la hipótesis de que esto podría estar relacionado con una alta inversión energética en adaptaciones morfológicas, lo que permitiría al camarón aferrarse al sustrato en las fuertes corrientes que habita. Además, la alta expectativa de vida, un fenómeno bien documentado en atyidos, podría permitir a las especies una menor inversión energética por camada de huevos, pero por un periodo de tiempo más prolongado.

Palabras clave: anfidromia, fecundidad, neotrópico, rendimiento reproductivo, Atlántico sudoccidental, Brasil.

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INTRODUCTION

Tropical and subtropical freshwater ecosystems host a vast diversity of invertebrate macrofauna, including decapod crustaceans as one of their prominent components (Bond-Buckup *et al.*, 2008; De Grave *et al.*, 2008; Yeo *et al.*, 2008). Caridean shrimps constitute a numerically important group of this macrofauna, dominated by the families Atyidae and Palaemonidae with about 1,450 species (469 and 981, respectively), currently recognized and distributed worldwide (De Grave & Fransen, 2011). Atyid shrimps are usually associated with rapidly flowing streams (Hobbs & Hart, 1982). Their life cycle is characterized by amphidromy, meaning that the adults live in freshwater habitats, but the larvae need coastal waters for their successful development (Hobbs & Hart, 1982; Bauer, 2011a). These amphidromous shrimps are considered as the dominant macro consumers in many tropical streams (March *et al.*, 1998), and particularly, the atyid shrimps are known to reduce sediment cover and algal standing crop, and influence insect and algal species composition (see March *et al.*, 1998, 2002).

Currently, four species of Atyidae have been recognized from Brazil, two species of the genus *Potimirim* Holthuis, 1954 and two of *Atya* Leach, 1816 (Melo, 2003; Torati & Mantelatto, 2012), both natives of Brazilian drainages. Among these species, only *Atya scabra* (Leach, 1815), commonly known as “horse shrimp” or “camacuto shrimp” in some regions, is commercially exploited by artisanal fishermen, mainly in the northern states of Brazil (Almeida *et al.*, 2010), but is also of economic value in Mexico, Venezuela and Puerto Rico (Buckup & Bond-Buckup, 1999; Martínez-Mayén & Román-Contreras, 2000; Melo, 2003; R. Bauer, *pers. comm.*). This species has a wide amphiatlantic distribution, occurring from Mexico southward (Guatemala, Honduras, Nicaragua, Costa Rica, Panama, Colombia, Venezuela) to Brazil (from Bahia to Rio Grande do Sul states), as well as across most Caribbean islands (Cuba, Jamaica, Haiti, Curacao, Trinidad) (Hobbs &

Hart 1982; Galvão & Bueno, 2000). In Africa, it occurs from Liberia southwards to Angola, as well as at Cape Verde Islands in the Gulf of Guinea (Hobbs & Hart, 1982; Melo, 2003; Mantelatto & De Grave, unpublished data). In the Neotropical region, studies concerning the reproductive ecology of *A. scabra* have focused on larval morphology (Abrunhosa & Moura, 1988), descriptions of ovarian development, seasonal presence of ovigerous females, general information on fecundity and egg size (Galvão & Bueno, 2000), and reproductive period, female size and fecundity (Almeida *et al.*, 2010). However, none of these studies considered different developmental egg stages, estimation of egg loss during embryogenesis and energy investment (reproductive output, RO; see Clarke *et al.*, 1991; Hines, 1991, 1992) in egg production. Considering this lack of information, the present study analyses such aspects to broaden knowledge about the reproduction of this amphidromous species. Such information might be of special importance to stimulate other studies, in different areas, considering the ongoing fragmentation of tropical streams, which might severely affect the life cycle of this migrating freshwater shrimp species (March *et al.*, 1998, 2003; Bauer, 2011b).

MATERIALS AND METHODS

Data were collected between July and September 2006, and January, May and July 2007 in São Sebastião Island, Brazil (Fig. 1). Individuals were captured using sieves in regions of strong currents, which were placed near overturned rocks. Details of abiotic conditions in the sampling area have been described by Mossolin *et al.* (2010).

Individuals were fixed in 80% EtOH; some of them for reference collections, and the remaining specimens were brought to the University of São Paulo (USP) for further analysis. Voucher specimens were deposited in the following crustacean collections: Museum of Zoology-University of São Paulo (MZUSP), and Faculty of Philosophy, Sciences and

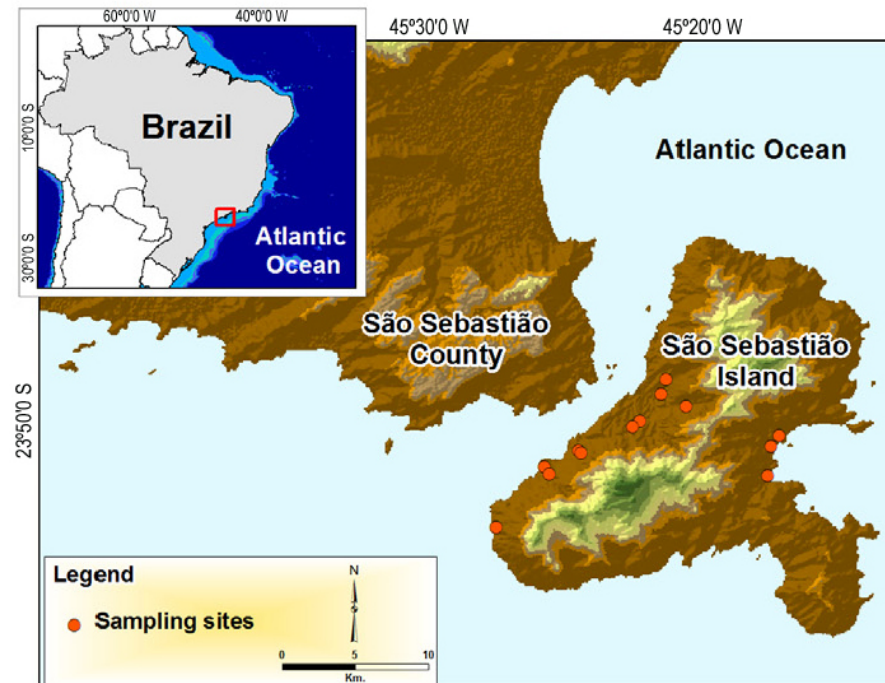


Figure 1. Sample sites where *Atya scabra* was collected (red points) in São Sebastião Island, Brazil (July 2006-July 2007).

Letters of Ribeirão Preto - FFCLRP, University of São Paulo (USP) (CCDB).

The carapace length (CL) (from the post-orbital margin to the dorsal posterior margin of the carapace) was measured with a digital caliper (0.01 mm precision). For the study of reproductive parameters, the entire mass of eggs was removed from each ovigerous female. Embryos were separated according to their stage of development (Stage I, homogeneous color within the egg, no eye pigments visible; Stage II, eye pigments barely visible; Stage III, eyes fully developed) (Wehrtmann, 1990). Thirty eggs from each ovigerous female were separated; their length and width was measured to calculate the egg volume (V), using the formula $V = 1/6 (\pi d_1^2 d_2)$ (Turner & Lawrence, 1979).

From the total mass of preserved eggs, three subsamples were taken. For each, eggs were counted, weighted and dried for approximately 12 h. From the remaining egg mass, only wet and dry mass was calculated. The same process was applied for the females in order to calculate the reproductive output by applying the formula $RO = \text{wet mass of the total egg batch of the female} / \text{wet mass of the female without the eggs}$ (Clarke *et al.*, 1991). The RO was estimated only for females with newly-extruded eggs (Stage I). Percent egg water content was calculated for all three embryonic developmental stages by the

following formula: $(\text{egg wet weight} - \text{egg dry weight}) * 100 / \text{egg wet weight}$ (Lardies & Wehrtmann, 2001; Lara & Wehrtmann, 2009; Wehrtmann *et al.*, 2012).

The nonparametric Kruskal-Wallis test was used to compare the values of volume and water content of embryos in different developmental stages (I, II and III).

RESULTS

In total, 65 sites were surveyed, and *Atya scabra* was collected in 13 of these locations (Fig. 1). A total of 74 individuals were obtained, comprising 14 males, 30 females without eggs, 21 ovigerous females and 9 juveniles.

Carapace length (CL) of ovigerous females (N = 21) ranged from 13.5 to 25.1 mm, with a mean size of 20.0 ± 3.02 mm CL. Females carrying Stage-II embryos were the largest with an average size of 22.2 mm CL, while females with embryos close to hatching (Stage III) showed the smallest average size with 17.9 mm CL (Table 1). Independent of the developmental stage of the eggs, fecundity varied between 414 and 19250 eggs (Table 1). The average fecundity (Stage I) was 8343 ± 4945.5 . The size (CL) was positively correlated with the number of Stage-I embryos (Fig. 2). The mean volume of eggs increased during embryogenesis from 0.027 ± 0.007 in Stage I to 0.055

Table 1. Size (carapace length: CL; total length: TL) of ovigerous females of *Atya scabra*, average egg volume, and water content of eggs per developmental stage. SD: standard deviation; N: number of individuals.

	Stage I	Stage II	Stage III
Female CL (mm)			
Average	20.0	22.2	17.9
± SD	2.8	2.4	3.4
Max.	25.1	25.0	20.9
Min.	16.5	20.8	13.5
Female TL (mm)			
Average	62.5	68.3	56.2
± SD	8.4	6.7	9.8
Max.	77.3	75.9	63.8
Min.	52.2	64.2	42.8
Egg volume (mm ³)			
Average	0.027	0.026	0.055
± SD	0.007	0.003	0.022
Max.	0.047	0.030	0.078
Min.	0.017	0.024	0.026
N	14	3	4

± 0.022 mm³ at the end of the incubation period (Stage III), which represented an overall egg volume increase of 103%. The volume of Stage-III embryos was significantly different from those in Stage I and II (Kruskal-Wallis: $H = 45.54$; $DF = 2$; $P < 0.05$). Average water content of the eggs increased during the incubation period continuously from 60.0% (Stage I) to 82.6% (Stage III); water content in Stage I was significantly lower than in more advanced stages (Kruskal-Wallis: $H = 37.53$; $DF = 2$; $P < 0.05$); however, there was only a significant increase in water content from the first to the second stage. During the incubation period (Stage I-III), females lost on average 15% of their initially produced eggs. The mean RO was $3.6 \pm 1.9\%$, and its values ranged from 1.0 to 6.9% (Fig. 3). There was no significant relationship between RO and CL of ovigerous females ($r = 0.03$; $P = 0.56$; $n = 14$).

DISCUSSION

Our data regarding reproductive aspects of *Atya scabra* showed an average fecundity substantially higher than two populations previously studied in São Sebastião, Brazil (Galvão & Bueno, 2000) and northeastern Brazil (Almeida *et al.*, 2010) (Table 2). Moreover, maximum egg numbers are also considerably higher in our study than those reported by the other two Brazilian studies (Table 2). These

differences, however, are most probably related to the size of the females analyzed in the respective studies, where the two previous reports for *A. scabra* analyzed much smaller females than those processed in the present study. Considering that fecundity in decapods usually increases with female size (for freshwater shrimps reported from Latin America: Reid & Corey, 1991; Anger & Moreira, 1998; Lara & Wehrmann, 2009; Tamburus *et al.*, 2012, and references cited in these publications), it is not surprising that our study revealed higher fecundity values as previous studies which analyzed smaller females of the same species.

Brood loss is a well-known phenomenon in decapods (for review: Kuris, 1991) and may vary in caridean freshwater shrimps between 23% (Anger & Moreira, 1998) and 53% (Balasundaram & Pandian, 1982). Information of egg mortality during embryogenesis in Atyidae is extremely limited. Darnell (1956) studied a population of *A. scabra* from Mexico and concluded that the species might lose 60% of their initially produced eggs. This value is considerably higher than our estimate (15%); however, and just as in the present study, calculations were based on a low number of individuals carrying embryos closed to hatching ($n = 3$; Darnell, 1956). Therefore, additional material, especially females with Stage-III eggs, needs to be analyzed before any solid conclusion can be made about brood loss in *A. scabra*.

The egg volume of *A. scabra*, in the present study, was slightly lower, but comparable to the values reported by Galvão & Bueno (2000) from the same study area (Table 2). However, eggs of *A. scabra* seems to be substantially smaller than those of *A. margaritacea* (Table 2). Inter- and intraspecific differences in egg size are a common phenomenon in decapods (for caridean shrimps see: Chow *et al.*, 1988; Anger & Moreira, 1998; Wehrmann & Kattner, 1998; Lardies & Wehrmann, 2001; Terossi *et al.*, 2010). Nevertheless, egg size is an indicator of energy allocation for reproduction (see Ramírez-Llodra, 2002), and it is especially important for the understanding of life history traits in amphidromous species, such as Atyidae (see Bauer, 2011a, 2011b; Bauer, 2013). The relatively small egg size of *A. scabra* is in agreement with the prolonged larval development of the species (11 zoeal stages, approx. 53 days; Abrunhosa & Moura, 1988), suggesting that the life cycle of this freshwater shrimp needs to include a coastal-marine phase for the successful development of the planktonic larvae (Hobbs & Hart, 1982; Covich *et al.*, 1996; Almeida *et al.*, 2010).

Egg volume of *A. scabra* more than doubled during the incubation period (Table 2). This is not uncommon in marine caridean shrimps (*e.g.*,

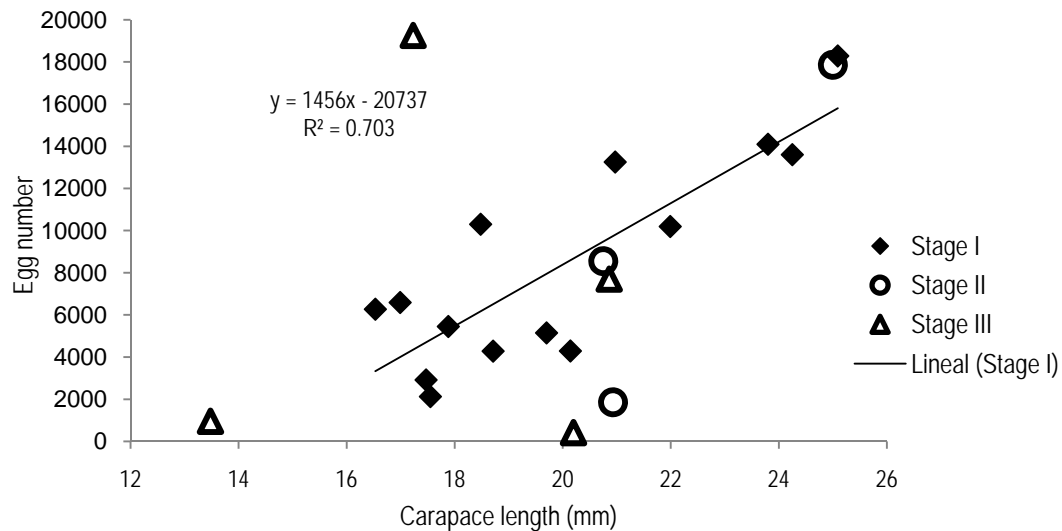


Figure 2. Number of eggs as a function of female size (CL) of *Atya scabra* (N = 21). The regression line refers to Stage-I eggs.

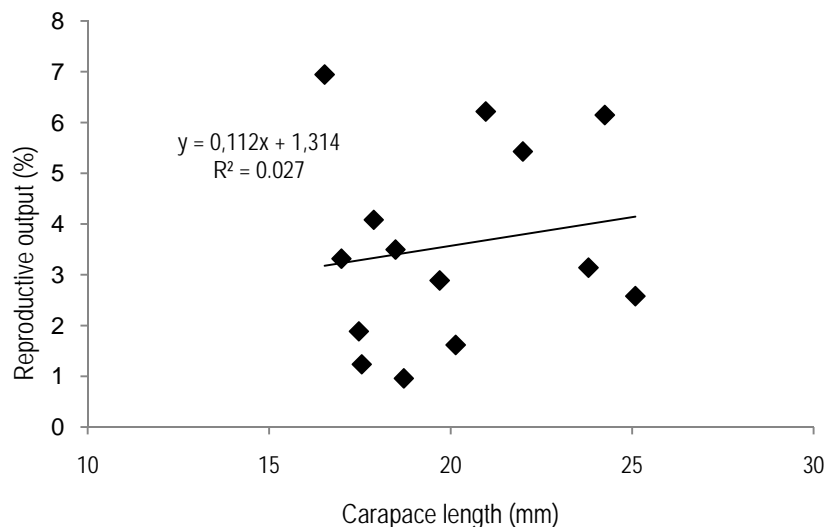


Figure 3. Reproductive output of female *Atya scabra* with newly extruded eggs (Stage I; N = 14) as a function of female size (CL).

Hippolytidae: Terossi *et al.*, 2010), but the available data for freshwater shrimp indicate considerably lower values: Lara & Wehrmann (2009) and Tamburus *et al.* (2012) compiled published data for egg volume increase in *Macrobrachium* spp. and reported values varying between 28% (*M. potiuna*; Nazari *et al.*, 2003) and 38% (*M. acanthurus*; Tamburus *et al.*, 2012). These values are in good agreement with those mentioned for the genus *Atya*: *A. scabra* [30.9%, calculated with egg size data presented by Galvão & Bueno (2000)] and for *A. margaritacea* (30.8%, calculated with egg size data presented by Martínez-

Mayén & Román-Contreras, 2000). While our data indicate a substantially higher egg volume increase compared to the above-mentioned studies, this may be associated with the fact that the analyzed material by us included eggs ready to hatch, and the egg swelling seems to be especially pronounced during this final part of the incubation period (Pandian, 1970; García-Guerrero & Hendrickx, 2006; Zhao *et al.*, 2007). However, and considering the low number of eggs revised in Stage III (n = 4) in this study, and the fact that neither Galvão & Bueno (2000) nor Martínez-Mayén & Román-Contreras (2000) indicated the

Table 2. Total length (TL), average fecundity and volume of eggs in Stage I and III from ovigerous females of *Atya scabra* and *A. margaritacea*.

Species	Female TL (mm)	Average fecundity (min-max)	Stage I-egg volume (mm ³)	Stage III-egg volume (mm ³)	Reference
<i>Atya scabra</i>	52.2-77.3	8343 (2124-18286)	0.027	0.055	Present study
<i>A. scabra</i>	25.3-61.1	3881 (324-11263)	0.034	0.044	Galvão & Bueno (2000)
<i>A. scabra</i>	33.0-58.0	3811 (870-8907)	---	---	Almeida <i>et al.</i> (2010)
<i>A. margaritacea</i>	32.0-66.0	1504-16200	0.018	0.023	Martínez-Mayén & Román-Contreras (2000)

number of eggs close to hatching analyzed, it might be premature to conclude on the increase of the egg volume during embryogenesis in *A. scabra*.

The uptake of water during embryogenesis is considered as the principal cause of egg volume increase observed in decapods (*e.g.*, Balasundaram & Pandian, 1982; Lardies & Wehrtmann, 1997; Müller *et al.*, 2004). Water content of *A. scabra* increased on average 22.6% which is slightly higher than values published for the freshwater shrimp *Macrobrachium carcinus*: Lara & Wehrtmann (2009) reported an increase of 15.8% in water content. Information regarding this aspect is not available for other atyid shrimps.

Pandian (1970) suggested that the water content of marine benthic decapods eggs, with planktonic larval development, increases from an initial 50-60% up to 70-80% at the end of the incubation period. Data of the freshwater shrimp *M. carcinus* showed similar values (from 66.3% to 82.6%; Lara & Wehrtmann, 2009), and the authors of that study speculated that the pattern described by Pandian (1970) may also be valid for benthic freshwater shrimp with planktonic development. The present data provide further support for this assumption: water content in *A. scabra* increased from 60.0% (Stage I) to 82.6% (Stage III). Thus, the available information may suggest that egg water content values are not substantially different between marine and freshwater benthic decapods with an extended larval period.

As far as we know, this is the first report of RO for any atyid shrimp. The energy allocation in egg production seems to be independent of the female size (Fig. 3), which is in agreement with similar observations in other caridean shrimps (Wehrtmann & Andrade, 1998; Wehrtmann & Lardies, 1999; Terossi *et al.*, 2010). The obtained value (RO: 3.6%) is considerably lower than previous reports for other freshwater shrimps: Mantel & Dudgeon (2005) reported for *M. hainansense* an average RO of 10.0%, and Lara & Wehrtmann (2009) 12.0% for *M. carcinus*. It is speculated that the habitat preference of *A. scabra*

may be related to the relatively low energy investment in egg production: according to Hobbs & Hart (1982), the presence of most *Atya* species is limited to rapidly flowing streams with high oxygen content. Moreover, the external morphology of the species shows adaptations, which allow the shrimp to cling on to the substrate in this fast flowing environment (see Almeida *et al.*, 2010). Therefore, we hypothesize that the development of these morphological adaptations, in association with costs/disadvantages of its amphidromous life style, may require a considerable energy investment, which in turn may reduce the amount of available energy for egg production. Additionally, considering that tropical atyid shrimp seems to have a surprisingly long life span (*Atya lanipes*: 8 years; Cross *et al.*, 2008), it might be hypothesized that *A. scabra* invest less energy per brood in egg production, but over a longer time span than many other freshwater carideans (Cross *et al.*, 2008; Vogt, in press).

Finally, as previously advised for comparative studies on reproduction of freshwater shrimps (Tamburus *et al.*, 2012), we cannot refute the possibility of intraspecific population variability. Further detailed studies on population genetics are in progress to compare in detail other populations along their range of distribution, including a latitudinal reproductive analysis to obtain more conclusive data about intraspecific variability of reproductive features of *A. scabra*.

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