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Research Article

Reproductive cycle and size at first sexual maturity of the white shrimp *Penaeus schmitti* (Burkenroad, 1936) in northeastern Brazil

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ABSTRACT. The present study aimed to investigate the reproductive cycle and size at first maturity of *Penaeus schmitti* through a macro and microscopic approach. Between August 2011 and July 2012, 1169 specimens were collected by an artisanal fishing vessel operating a double trawl off the coast of Pernambuco, northeast Brazil. The total proportion of males (42%) was significantly lower than females (58%), corresponding to the sex ratio of 1:1.38. The total body length at first ovarian maturation (TL_{50}) in females was estimated at 14.2 cm. The ovarian development was divided into four distinct stages based on histological characteristics and visual observations. This is the first reported occurrence of vitellogenic oocytes in the spent stage of *P. schmitti*, indicating a rapid ovarian maturation after spawning. Furthermore, the frequency of maturation stages, diameter of oocytes and gonadosomatic index were distributed homogeneously throughout the study period, reinforce a continuous reproductive cycle for *P. schmitti* population in northeastern Brazil.

Keywords: reproductive cycle, ovarian maturation, length at first maturity, gonadosomatic index, penaeid, crustacean.

INTRODUCTION

The penaeids are the most abundant (67%) crustacean fishery resource in the Brazilian coast, with the white shrimp *Penaeus schmitti* (= *Litopenaeus schmitti*) (Burkenroad, 1936), representing 7% of the total catch (MPA, 2012). In northeast Brazil, approximately 100,000 people depend directly or indirectly on the fishery of these crustaceans for their living (Santos *et al.*, 2006). However, no effective measures for the regulation of shrimp trawling are available now in Pernambuco, in contrast with other Brazilian states, where there is regulatory legislation (Lopes *et al.*, 2014).

The white shrimp is distributed in the Greater Antilles and Atlantic coast of Central and South America from British Honduras to southern Brazil (FAO, 1980). As observed in most penaeids, its life cycle is carried out in two ecosystems, during which the post-larvae drift on ocean currents until they reach an estuary, where they develop into the juvenile stage, before migrating back to the ocean, where they become adults (Dall *et al.*, 1990; Coelho & Santos, 1993; Santos *et al.*, 2006). Juveniles and adults prefer muddy-sandy substrates at depths of up to 50 m (Pérez-Farfante, 1970).

Penaeid populations tend to present continuous reproduction with or without seasonal peaks, which could be influenced by environmental factors and geographical locations (Staples & Rothlisberg, 1990; Coelho & Santos, 1995). However, the reproductive cycle of *P. schmitti* based on the relationship between macro and microscopic features during the ovarian maturation have been reported only to *P. schmitti* populations in southern Brazil (Gonçalves *et al.*, 2009; Machado *et al.*, 2009). Furthermore, data on reproductive dynamics, including gonadal development and

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size at first gonadal maturity are important parameters for the development of effective conservation strategies to monitor and control fishery activities in specific areas (Carbonell *et al.*, 2006; Machado *et al.*, 2009; Kevrekidis & Thessalou-Legaki, 2013).

The present study aimed to investigate the reproductive cycle and size at first maturity of *P. schmitti* through a macro and microscopic approach, as well as help to improve the overall sustainability of this species by contributing to the elaboration of guidelines for the shrimp fishery in the northeast Brazil.

MATERIALS AND METHODS

Study area and sampling

The study area was located near the mouth of the Sirinhaém River (8º35'-8º36'S and 34º56'-35º00'W), one of the most important fishing grounds in Pernambuco state, northeastern Brazil.

During the period from August 2011 through July 2012, *P. schmitti* were caught monthly by trawling during the day in the full moon phase, using 10 m long double trawl nets with a 6.10 m mouth, 30 mm mesh in the body and 25 mm mesh in the tail of the net. The specimens were collected in three trawls of two hours, with approximately 50 shrimp being selected at random from each trawl. Once selected, the specimens were immediately stored on ice until analysis.

Population structure

The sex of each specimen was determined by the presence of the thelycum and petasma, for females and males respectively. The total body length (TL: from the tip of the rostrum to the extremity of the telson) were measured using a digital caliper (mm) and total wet weight (TW) was recorded on an analytical balance (0.1 g precision). The homogeneity of the sex ratio within length classes and months was analyzed by Chi-square test (χ^2) with correction of Yates (Snedecor & Cochram, 1980).

Ovarian development

Firstly, the ovarian development was evaluated every month based on the gonadosomatic index (GSI = ovary weight/TW × 100%), morphology and coloration of the gonads. The color of the fresh ovary was compared with a widely available chromatic scale to determine the most frequent color observed in the ovaries (Pantone, 1999) Matching System, Pantone, Carlstadt, NJ, USA).

For the histological analysis, samples of the median portion of the ovary were collected from 20 specimens in different macroscopic maturation stages (Machado *et al.*, 2009). The tissue was fixed in Davidson solution for 24 h and then transferred to 70% ethanol before being set in paraffin at 58ºC, sectioned (6 µm) and stained with Hematoxylin-Eosin (Bell & Lightner, 1988). The histological sections were observed under a microscope coupled to a camera connected to a computer for the capture and digitalization of a series of images of the different fields of each section.

The oocytes were classified according to their histological characteristics, based on the descriptions proposed by Gonçalves *et al.* (2009) and Machado *et al.* (2009). The proportion of each type of oocyte was calculated for each month, and 30 oocytes representing each category (or the total number available, if less than 30) were measured using Image Tool 2.0 for Windows (The University of Texas Health Science Center in San Antonio, TX, USA). Only oocytes with nuclei sectioned in the equatorial plane were selected for this analysis. The data were grouped into distinct maturation stages according to the most developed cell observed in each sample.

Data on GSI, frequency, and diameter of each type of oocyte were compared among maturation stages and during the sample period (group bimonthly) by one-way analysis of variance (ANOVA) followed by Tukey test at significance level of 95%.

Reproductive cycle and length at first maturity

The size at first ovarian maturation was determined by plotting the relative frequency of females in each 0.5 cm size class. Specimens were considered to be an adult when they presented well-developed or spent gonads. Body length classes were then plotted against the percentage of adult females, adjusted by the iterative non-linear least squares technique to obtain the value of L_{50} using the logistic equation described by King (1995):

$$P = 1 / [1 + \exp(-r\,(TL-TL_{50}))]$$

where *P:* the percentage of mature females in the total length class, r: slope of the curve, TL: upper limit of the total length class, and TL_{50}: mean total length at first maturation.

The maturity of the males was determined by the joining of the petasma (joined: mature, unjoined: immature), and the presence of spermatophores in the terminal ampules (Dall *et al.*, 1990).

RESULTS

Throughout the year, 1169 specimens were collected, except for January when no *P. schmitti* was found. The total proportion of males (42%) was significantly lower than females (58%), corresponding to the sex ratio of 1:1.38 (Table 1).

Table 1. The monthly and total sex ratio for males and females of *Penaeus schmitti* captured during the period of August 2011 to July 2012, off the coast of Pernambuco, Brazil. Asterisks indicate significant difference ($P < 0.05$) in sex ratio. NP: indicates months that individuals were not present in the sample.

Months	Male	Female	Total	Ratio	$P < 0.05$
August	39	73	112	1: 1.87	0.001*
September	35	86	121	1: 2.46	0.000*
October	49	58	107	1: 1.18	0.384
November	45	19	64	1: 0.42	0.001*
December	43	75	118	1: 1.74	0.003*
January	NP	NP	-	-	-
February	32	45	77	1: 1.41	0.138
March	22	49	71	1: 2.23	0.001*
April	20	44	64	1: 2.20	0.003*
May	36	59	95	1: 1.64	0.019*
June	104	97	201	1: 0.93	0.621
July	66	73	139	1: 1.11	0.553
Total	491	678	1169	1: 1.38	0.000*

The total body length range for females (8.6 to 20.9 cm) was higher in comparison with males (9.7 to 16.5 cm). Although both sexes showed higher relative frequency at the size class of 12.5-13.5 cm, the number of males was significantly higher than females. However, the relative frequency of females was significantly higher at larger size classes (Fig. 1).

Based on histological characteristics and visual observations, the ovarian development was divided into four distinct stages:

Stage I (immature): predominance of basophilic oocytes (BO) with large nucleus surrounded by a number of nucleoli and mean diameter of 38.46 ± 11.32 µm (Fig. 2a, Table 2). The gonads are very thin and flaccid, which impairs their visualization through the exoskeleton. The ovary color varies from translucent to cream (587 PC).

Stage II (maturing): vitellogenic oocytes (VO) with a mean diameter of 123.47 ± 9.29 µm are distributed in the periphery of the ovarian lobes. The BO is found primarily in the central region with a frequency of 71.4% (Fig. 2b, Table 2). At this stage, the ovary can be visualized through the exoskeleton as it fills the abdominal cavity and covers part of the intestine in the cephalothorax region. The ovary color is light yellow (393 PC).

Stage III (mature): the presence of mature oocytes (MO) with peripheral cortical rods, which indicate the final stage of maturation (Fig. 2c). The BO has a mean diameter of 201.32 ± 9.39 µm and frequency of 65.0% (Table 2). The gonads are easily seen, as the lateral and posterior lobes occupy the whole of the cephalothorax and abdominal cavity, respectively. At this stage, the ovary is dark green in color (396 PC).

Stage IV (spent): this stage differs microscopically from stage I by the presence of atretic oocytes (AO), which are mature oocytes in the process of being reabsorbed. In addition to these cells, is also possible to observe BO and VO with the frequency of 97.7% and 1.6%, respectively (Fig. 2d, Table 2). Macroscopically, the coloration of the ovary is equivalent to that of stage I.

There were no significant differences in total body length of females among ovarian development stages, but the GSI was significantly higher in stage III (Table 2). Basophilic oocytes (BO) were observed in all ovarian development stages without significant variations in their mean diameter. However, these oocytes were most abundant in stages I, and IV, differing significantly from the stages II and III (Table 2). The presence of VO was observed in the stages II and IV, but with significantly higher proportion and diameter in the maturing stage. In contrast, the presence of MO and AO was exclusive of the mature and spent stages, respectively (Table 2).

From the total number of ovaries analyzed microscopically, 20.4% were immature (I), 42.5% maturing (II), 31.9% mature (III) and 5.3% spent (IV). The distribution of the ovarian development stages during the year (group bimonthly) did not show significant differences (Fig. 3). A similar pattern was observed for the mean diameter of each oocyte type (Fig. 4) and GSI values (Fig. 5), which also did not vary significantly throughout the study period.

The total body length at first gonadal maturation (TL_{50}) of the females was estimated at 14.2 cm (Fig. 6). The smallest TL for mature females was 11.16 cm, whereas all those above 19 cm were classified as matures. Regardless the size, all males were considered mature (*i.e.*, joined petasma and presence of spermatophores) throughout the study period.

DISCUSSION

The sex ratio of 1:1.38 (male:female) observed in the present study is within the range reported for *Penaeus schmitti* populations in different locations along the northeast (Santos *et al.*, 2005) and southeast (Santos *et al.*, 2008) coast of Brazil. The similar sex ratio of 1:1.2 (male:female) was also reported for *P. schmitti* in Venezuela by Glenys *et al.* (1999). However, Coelho & Santos (1995) observed a higher proportion of *P. schmitti* males (53.2%) than females (46.8%) in the vicinity of the mouth of the São Francisco River,

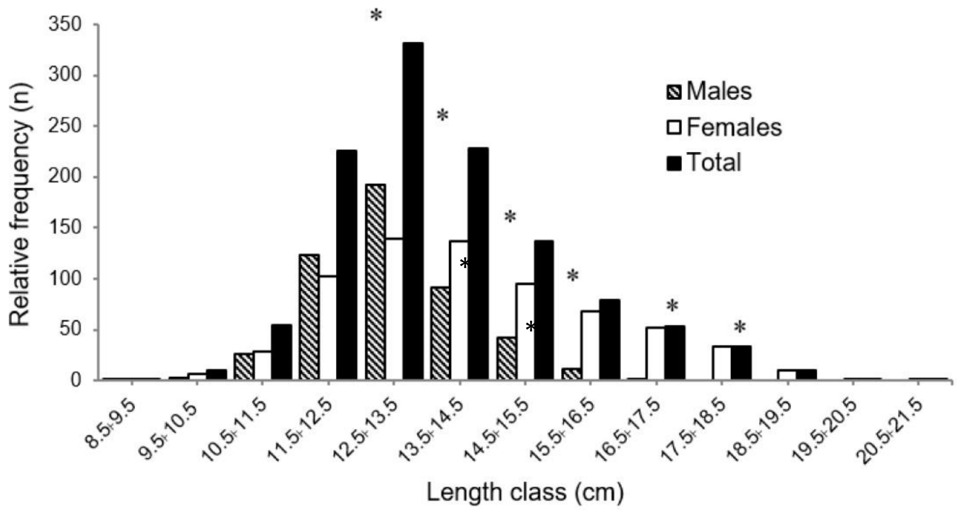

Figure 1. Distribution of the relative frequency per total body length classes of males, females, and total (pooled sexes) of *Penaeus schmitti* captured off the coast of Pernambuco, Brazil. Asterisks indicate significant difference ($P < 0.05$) between the relative frequency of males and females in the length class.

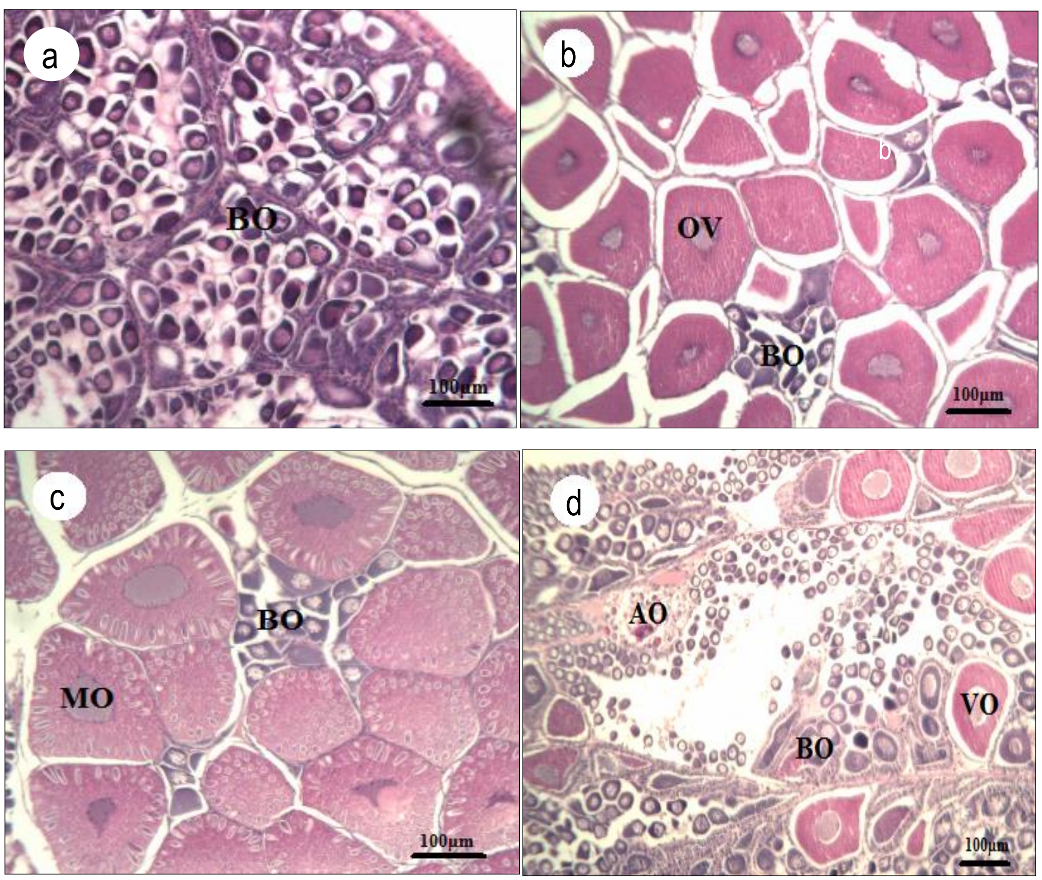

Figure 2. Histological sections (100x) of ovarian developmental stages of *Penaeus schmitti*. a) Stage I (immature) with total dominance of basophilic oocytes (BO), b) Stage II (maturing) with vitellogenic oocytes (VO) and BO restrict to the central region of the ovarian lobes, c) Stage III (mature) oocytes (MO) with peripheral cortical rods and BO in the central region of the ovarian lobes, d) Stage IV (spent) differs from stage I by the presence of atretic (AO) and vitellogenic (VO) oocytes.

Table 2. Mean (±SD) frequency and diameter of oocytes types (BO: basophilic, VO: vitellogenic, MO: mature and VO: atretic), gonadosomatic index (GSI) and total body length (TL) for each maturation stage (I to IV) of *Penaeus schmitti* females. Values in the same line marked with different letters are significantly different (P < 0.05). NP: indicates that oocytes were not present.

	Stage I	Stage II	Stage III	Stage IV
BO (%)	100[a]	71.37 ± 3.43[b]	64.95 ± 4.49[c]	97.74 ± 0.86[a]
VO (%)	0[b]	28.63 ± 3.43[a]	0[b]	1.64 ± 0.75[b]
MO (%)	0[b]	0[b]	35.05 ± 4.49[a]	0[b]
AO (%)	0[b]	0[b]	0[b]	0.62 ± 0.13[a]
BO (µm)	38.46 ± 11.32[a]	36.51 ± 5.71[a]	37.07 ± 6.79[a]	32.45 ± 4.44[a]
VO (µm)	NP	123.47 ± 9.29[a]	NP	95.9 ± 4.98[b]
MO (µm)	NP	NP	201.32 ± 9.39	NP
GSI (%)	1.40 ± 0.38[b]	3.95 ± 1.61[b]	7.74 ± 1.59[a]	2.57 ± 1.48[b]
TL(cm)	13.28 ± 1.88[a]	14.57 ± 1.79[a]	14.94 ± 1.65[a]	16.6 ± 1.83[a]

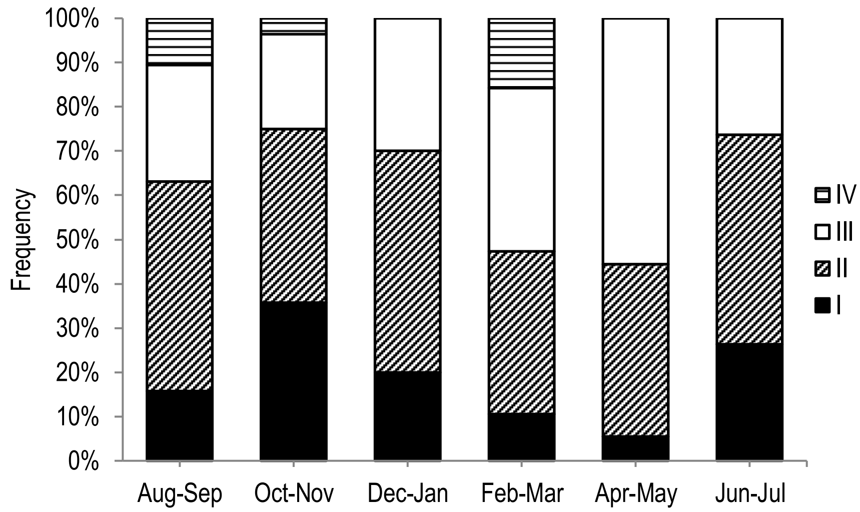

Figure 3. The frequency of ovarian development stages (I: immature, II: developing, III: mature and IV: spent) of *Penaeus schmitti* captured during the period of August 2011 to July 2012 (bimonthly grouped), off the coast of Pernambuco, Brazil.

northeast Brazil, which differs from our results of 42% males and 58% females in the mouth of the Sirinhaém River.

The higher proportion of females recorded in the present study appears to be characteristic of spawning grounds in the open sea for *P. schmitti* populations, whereas a sex ratio close to 1:1 may indicate an area in which mating occurs (Coelho & Santos, 1993, 1995). Our results also indicated that females present a significantly higher relative frequency in larger size classes, which have been previously reported for *P. schmitti* populations (Santos *et al.*, 2005, 2008). Penaeid females are larger than males due to the body space needed for gonadal development (Hartnoll, 1982; Dall *et al.*, 1990) and thus more abundant in larger size classes (García & Le Reste, 1986) Studies of ovarian development in penaeids have been used as a tool for the establishment of guidelines for fishery management (Quintero & Gracia, 1998), as well as the improvement of breeding technology for aquaculture operations (Peixoto *et al.*, 2003; Dumont *et al.*, 2007; Gonçalves *et al.*, 2009; Machado *et al.*, 2009). Histological analyses of the ovaries are considered to be one of the most accurate procedures for the determination of the maturational stage of female crustaceans (Ohtomi *et al.*, 2003; Carbonell *et al.*, 2006). This approach may guarantee greater reliability for the determination of the maturation stage, given the precision in identification of the different developmental stages and the potential for comparisons with features observed macroscopically, such as the morphology and coloration of the gonad (Quintero & Garcia, 1998; Peixoto *et al.*, 2003; Machado *et al.*, 2009).

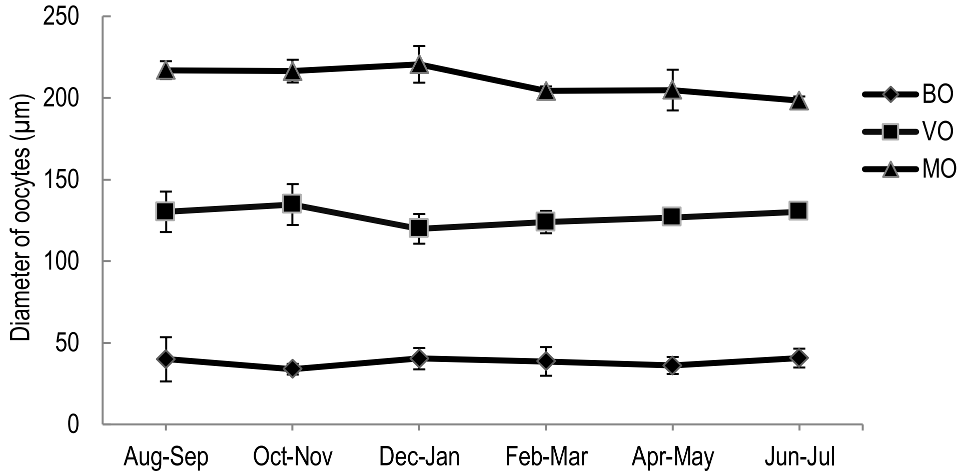

Figure 4. Mean diameter (±SD) of basophilic (BO), vitellogenic (VO) and mature oocytes (OM) of *Penaeus schmitti* captured during the period of August 2011 to July 2012 (bimonthly grouped), off the coast of Pernambuco, Brazil.

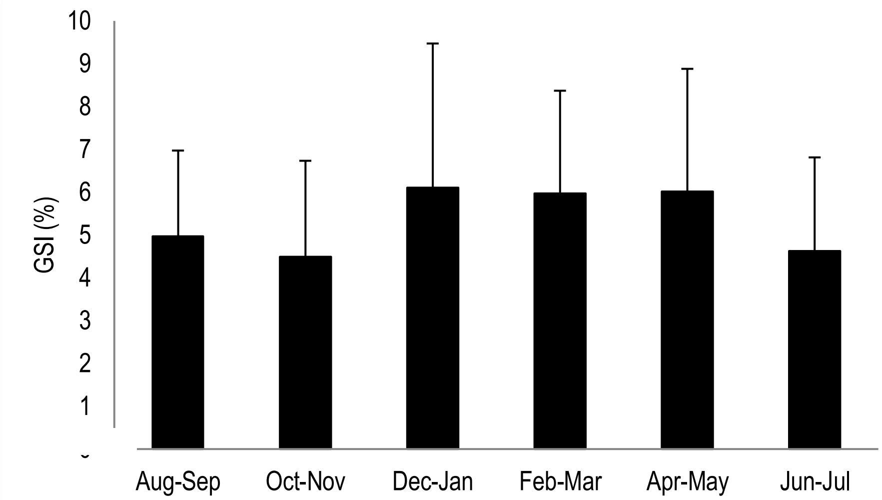

Figure 5. Mean (±SD) gonadosomatic index (GSI) of *Penaeus schmitti* females captured during the period of August 2011 to July 2012 (group bimonthly), off the coast of Pernambuco, Brazil.

The stages of ovarian maturation in penaeids have been defined according to the presence or absence of basophilic, vitellogenic, mature, and atretic oocytes (Quintero & Gracia, 1998; Peixoto *et al.*, 2003; Dumont *et al.*, 2007). These criteria were also adopted in the present study for the classification of the ovarian development of *P. schmitti*, which is in accordance with previous descriptions for this species in the southeast (Gonçalves *et al.*, 2009) and southern Brazil (Machado *et al.*, 2009). Although the overall ovarian development of *P. schmitti* in southern Brazil was similar to our results in terms of development stages and respective oocyte diameters, a major difference was the presence of vitellogenic oocytes in the spent stage suggesting a rapid ovarian maturation soon after spawning. Furthermore, the absence of mature oocytes in the spent ovaries indicates a reproductive strategy of total spawning followed by a new and continuous ovarian development cycle for *P. schmitti* population in our research area.

The continuous reproductive cycle of *P. schmitti* is reinforced by the homogeneous distribution of ovarian maturation stages, the diameter of oocytes and IGS throughout our study period. Previous studies have suggested a bimodal reproductive pattern for *P. schmitti* in northeast Brazil, based on a higher proportion of mature females in two distinct periods of the year (Coelho & Santos, 1993, 1995; Santos, 2000; Santos *et al.*, 2005). Nevertheless, these studies have used only macroscopical features to determine the maturation

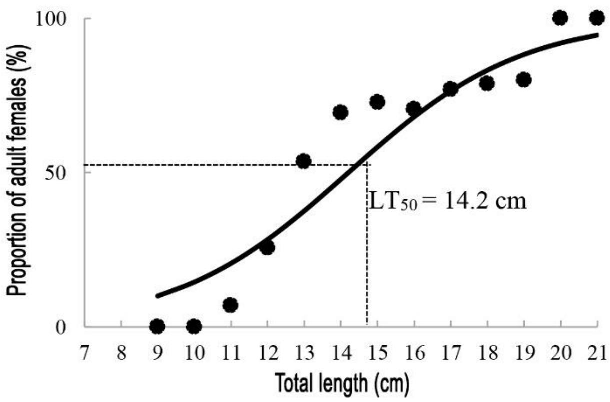

Figure 6. Total length, at first sexual maturity (LT_{50}), of *Penaeus schmitti* females captured during the period of August 2011 to July 2012 (grouped bimonthly), off the coast of Pernambuco, Brazil.

stages, which could lead to misinterpretation of the reproduction cycle of *P. schmitti* in the region.

A number of studies have found that the reproductive cycle of penaeid shrimp is typically defined by the maturation of the females (Quintero & Gracia, 1998; Crocos *et al.*, 2001; Cha *et al.*, 2002; López-Martínez *et al.*, 2005; Yamada *et al.*, 2007). Therefore, few analyses have focused on the maturity of the males, in which the size at first maturity can be defined by the proportion of specimens with joined or unjoined petasma (Costa & Fransozo, 2004; Sobrino & García, 2007). In aquaculture research, by contrast, the analysis of the reproductive condition of the males are more detailed (Ceballos-Vázquez *et al.*, 2003; Braga *et al.*, 2010; Silva *et al.*, 2015a).

Male penaeids tend to reach sexual maturity at a smaller body size than females (Boschi, 1969) and present spermatic reserves regardless the period of the year (Duffy & Thiel, 2007). All males sampled in this study were mature and had spermatophores in the terminal ampoule throughout the year. However, contrasting information is reported for *P. schmitti* in southeast Brazil, regarding the observation of males with joined petasma during specific periods (Simões, 2012) or throughout the year (Santos *et al.*, 2008).

The length at first maturity in penaeids may vary depending on the region due to environmental factors, such as seasonality, latitude, and water depth (Dall *et al.*, 1990). In addition, increased fishing pressure can alter life history characteristics, such as growth and size/age at maturity (Lappalainen *et al.*, 2016). Machado *et al.* (2009) estimated in 15.2 cm the total length at first maturity of *P. schmitti* females in southern Brazil, whereas in the present study it was 14.2 cm. Such small difference is probably related to the higher water temperature of coastal waters in the northeast region, which could increase the growth rate and promote a premature maturation of *P. schmitti* in this region.

The target species (*Penaeus subtilis*, *Xiphopenaeus kroyeri*, and *P. schmitti*) caught by trawlers in the south coast of Pernambuco, are either close or at maximum exploitation rates (Lopes *et al.*, 2014; Silva, 2015b). This fishery is hence increasingly vulnerable in the future due to the lack of adequate regulatory legislation in the study area. Therefore, the present findings on the continuous reproductive strategy and size at first maturity will help the fishery management, especially in periods of recruitment and breeding of *P. schmitti* population in northeast Brazil.

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REFERENCES

Bell, T.A. & D.V. Lightner. 1988. A handbook of normal penaeid shrimp histology. World Aquaculture Society, Baton Rouge, 114 pp.

Boschi, E.E. 1969. Estudio biológico pesquero del camarón *Artemesia longinaris* Bate de Mar del Plata. Bol. Inst. Biol. Mar., Mar del Plata, 18: 1-47.

Braga, A.L., C.L. Nakayama, J.G. Martins, E.P. Colares & W. Wasielesky. 2010. Spermatophore quality of the pink shrimp *Farfantepenaeus paulensis* (Decapoda, Dendrobranchiata) broodstock fed with different maturation diets. Aquaculture, 307: 44-48.

Carbonell, A., A. Grau, V. Laurence & C. Gomez. 2006. Ovary development of the red shrimp, *Aristeus antennatus* (Risso, 1816) from the Northwestern Mediterranean Sea. Crustaceana, 79: 727-743.

Ceballos-Vázquez, B.P., C. Rosas & I.S. Racotta. 2003. Sperm quality in relation to age and weight of white shrimp *Litopenaeus vannamei*. Aquaculture, 228: 141-151.

Cha, H.K., C.W. Oh, S.Y. Hong & K.Y. Park. 2002. Reproduction and population dynamics of *Penaeus chinensis* (Decapoda: Penaeidae) on the western coast of Korea, Yellow Sea. Fish. Res., 56: 25-36.

Coelho, P.A. & M.C.F. Santos. 1993. Época da reprodução do camarão branco, *Penaeus schmitti* Burkenroad

(Crustacea, Decapoda, Penaeidae) na região de Tamandaré, PE. Bol. Tecn. Cient. Cepene, 1: 157-169.

Coelho, P.A. & M.C.F. Santos. 1995. Época de reprodução dos camarões *Penaeus schmitti* Burkenroad, 1936 e *Penaeus subtilis* Pérez-Farfante, 1967 (Crustacea, Decapoda, Penaeidae), na região da foz do rio São Francisco. Bol. Tecn. Cient. Cepene, 3: 122-140.

Costa, R.C. & A. Fransozo. 2004. Reproductive biology of the shrimp *Rimapenaeus constrictus* (Stimpson, 1874) (Crustacea, Decapoda, Penaeidae) in Ubatuba region, SP, Brazil. J. Crustacean Biol., 24: 274-281.

Crocos, P.J., Y.C. Park, D.J. Die, K. Warburton & F. Manson. 2001. Reproductive dynamics of endeavour prawns, *Metapenaeus endeavour* and *M. ensis*, in Albatros Bay, Gulf of Carpentaria, Australia. Mar. Biol., 138: 63-75.

Dall, W., B.J. Hill, P.C. Rothlisberg & D.L. Staples. 1990. The biology of the Penaeidae. Advances in Marine Biology, Academic Express, London, 489 pp.

Duffy, J.E. & M. Thiel (eds.). 2007. Evolutionary ecology of social and sexual systems: Crustaceans as model organisms. Oxford University Press, Oxford, 502 pp.

Dumont, L.F.C., F. D'Incao, R.A. Santos, S. Maluche & L.F. Rodrigues. 2007. Ovarian development of wild pink prawn (*Farfantepenaeus paulensis*) females in the northern coast of Santa Catarina State, Brazil. Nauplius, 15: 65-71.

Food and Agriculture Organization (FAO). 1980. Species Catalogue - shrimps and prawns of the world. An annotated catalog of species of interest to fisheries. FAO Fisheries Synopsis, Rome, 125 pp.

García, S. & L. Le Reste. 1986. Ciclos vitales, dinámica, explotación y ordenación de las poblaciones de camarones peneidos costeros. FAO Fish. Tech. Pap., 206 pp.

Glenys, J.A.P. & B.S.U. Wolfgang. 1999. Crecimiento y mortalidade del camaron blanco (*Penaeus schmitti*) em el Lago de Maracaibo, Venezuela. Zootec. Trop., 17: 63-89.

Gonçalves, S.M., J.L. Santos & E.S. Rodrigues. 2009. Estágios de desenvolvimento gonadal de fêmeas do camarão-branco *Litopenaeus schmitti* (Burkenroad, 1936), capturadas na região marinha da Baixada Santista. Rev. Ceciliana, 1: 96-100.

Hartnoll, R.G. 1982. Growth. In: D. Bliss (ed.). The biology of Crustacea: embryology, morphology, and ecology. Academic Press, New York, 2: 111-185.

Kevrekidis, K. & M. Thessalou-Legaki. 2013. Reproductive biology of the prawn *Melicertus kerathurus* (Decapoda: Penaeidae) in Thermaikos Gulf (N. Aegean Sea). Helgol. Mar. Res., 67: 17-31.

King, M. 1995. Fisheries biology, assessment, and management. Fishing Books News, Oxford, 346 pp.

Lappalainena, A., L. Saks, M. Sustarc, O. Heikinheimo, K. Jürgens, E. Kokkonen, M. Kurkilahti, A. Verliin & M. Vetema. 2016. Length at maturity as a potential indicator of fishing pressure effects on coastal pikeperch (*Sander lucioperca*) stocks in the northern Baltic Sea. Fish. Res., 174: 47-55.

Lopes, D.F.C., S. Peixoto & F.L. Frédou. 2014. Population biology of seabob-shrimp *Xiphopenaeus kroyeri* (Heller, 1862) captured on the south coast of Pernambuco State, northeastern Brazil. Braz. J. Oceanogr., 62: 331-340.

López-Martínez, J., F. Arreguín-Sánchez, S. Hernández-Vázquez, A.R. García-Juárez & W. Valenzuela-Quiñonez. 2003. Interannual variation of growth of the brown shrimp *Farfantepenaeus californiensis* and its relation to temperature. Fish. Res., 61: 95-105.

Machado, I.F., L.F.C. Dumont & F. D'Incao. 2009. Stages of gonadal development and mean length at first maturity of wild females of white shrimp (*Litopenaeus schmitti* - Decapoda, Penaeidae) in Southern Brazil. Atlântica, 31: 169-175.

Ministério da Pesca e Aquicultura (MPA). 2012. Boletim Estatístico da Pesca e Aquicultura. Ministério da Pesca e Aquicultura, Brasília, 129 pp.

Ohtomi, J., T. Tashiro, S. Atsuchi & N. Kohno. 2003. Comparison of spatiotemporal patterns in reproduction of the kuruma prawn *Marsupenaeus japonicus* between two regions having different geographical conditions in Kyushu, southern Japan. Fish. Sci., 69: 505-519.

Pantone. 1999. Pantone Professional Color System. 14th New Jersey, Carlstadt, 260 pp.

Peixoto, S., R.O. Cavalli, F. D´Incao, A.M. Milach & W. Wasielesky. 2003. Ovarian maturation on wild *Farfantepenaeus paulensis* relation to histological and visual changes. Aquacult. Res., 34: 1255-1260.

Perez-Farfante, I. 1970. Sinopsis de dados biológicos sobre el camarón blanco *Penaeus schmitti* Burkenroad, 1936. FAO Fish. Rep., 37: 1417-1438.

Quintero, M.E.S. & A. Garcia. 1998. Stages of gonadal development in the spotted pink shrimp *Penaeus brasiliensis*. J. Crustacean Biol., 18: 680-685.

Santos, M.C.F. 2000. Biologia e pesca de camarões marinhos ao largo de Maragogi (Alagoas- Brasil). Bol. Tecn. Cient. Cepene, 8: 7-37.

Santos, M.C.F., J.A. Pereira & C.T.C. Ivo. 2005. Dinâmica reprodutiva do camarão branco, *Litopenaeus schmitti* (Burkenroad, 1936) (Crustacea, Decapoda, Penaeidae), no Nordeste do Brasil. Bol. Tecn. Cient. Cepene, 13: 27-45.

Santos, M.C.F., J.A. Pereira, C.T.C. Ivo & R.F. Souza. 2006. Crescimento do camarão branco *Litopenaeus schmitti* (Burkenroad, 1936) (Crustacea, Decapoda, Penaeidae) no Nordeste do Brasil. Bol. Tecn. Cient. Cepene, 14: 59-70.

Santos, J.L., E. Severino-Rodrigues & A.M. Vaz-Dos-Santos. 2008. Estrutura populacional do camarão-branco *Litopenaeus schmitti* nas regiões estuarina e marinha da baixada santista, São Paulo, Brasil. Bol. Inst. Pesca, São Paulo, 34: 375-389.

Silva, E.F.B., N. Calazans, A. Mariano, S. Silva, M. Guerra & S. Peixoto. 2015a. Use of fluorescent microscopy for sperm quality of penaeids. J. Crustacean Biol., 35: 26-29.

Silva, E.F.B., N. Calazans, L. Nole, A. Viana, R.B. Soares, S. Peixoto & F.L. Fredou. 2015b. Population dynamics of the pink shrimp *Farfantepenaeus subtilis* (Pérez-Farfante, 1967) in northeastern Brazil. J. Crustacean Biol., 35: 132-139.

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Simões, S.M. 2012. Estrutura da comunidade e biologia reprodutiva de camarões marinhos (Penaeidea e Caridea), no Complexo Baia-Estuario de Santos e São Vicente/SP, Brasil. Thesis Doctorado, Estate University of São Paulo, Botucatu, 149 pp.

Snedecor, G.W. & E.G. Cochram. 1980. Statistical methods. Iowa State University Press, Ames, 476 pp.

Sobrino, I. & T. García. 2007. Reproductive aspects of the rose shrimp *Parapenaeus longirostris* (Lucas, 1846) in the Gulf of Cadiz (southwestern Iberian Peninsula). Bol. Inst. Esp. Oceanogr., 23: 57-71.

Staples, D.J. & P.C. Rothlisberg. 1990. Recruitment of penaeid prawns in the Indo-West Pacific. In: R. Hirano & I. Hanyu (eds.). The second Asian fisheries forum. Asian Fisheries Society, Manila, pp. 847-850.

Yamada, R., K. Kodama, T. Yamakawa, T. Horiguchi & I. Aoki. 2007. Growth and reproductive biology of the small penaeid shrimp *Trachysalambria curvirostris* in Tokyo Bay. Mar Biol., 151: 961-971.