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Gonad development in the commercially exploited deepwater shrimp *Solenocera agassizii* (Decapoda: Solenoceridae) from Pacific Costa Rica, Central America

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ABSTRACT

Commercial fisheries are going deep and the lack of life history data of the exploited deepwater species is considered a major limitation for the development and implementation of adequate management measures. *Solenocera agassizii* is a deepwater shrimp commercially exploited along the Pacific coast of Costa Rica; however, its reproductive biology is completely unknown. Therefore, this study was conducted to describe the ovarian development of this solenocerid species to facilitate the development of urgently needed management plans. Based on the relationship between macroscopic (color and ovary size) and microscopic (cell type) characteristics, four stages of ovarian development were determined (immature, previtellogenic, vitellogenic and mature) for the females of *S. agassizii*. A reabsorbing/spent ovary was not found. The four stages found can be grouped in "not visible" and "visible" based on the observation of the ovary through the exoskeleton in fresh specimens. These specimens can easily be used for a simple and rapid assessment of the gonad development in the field. Oocyte diameters ranged from 56.2 μm (Stage I) to 255.4 μm (Stage IV), and GSI (Gonadosomatic index) values varied between 0.36% (Stage I) and 6.65% (Stage IV). The classification obtained in this study was supported by coefficient of variance values and significant differences among stages, oocyte diameters and GSI values during the ovarian development. Therefore, we are confident that the combination of microscopic and macroscopic characteristics allows the establishment of easily recognizable developmental stages of the gonad in *S. agassizii*, which may be an important tool for future monitoring of the reproductive status of the population.

1. Introduction

Fish catches have been declining worldwide, mainly due to the overexploitation of shallow water resources (Jackson et al., 2001; Gillett, 2008). Consequently, commercial fleets now tend to fish in deeper waters (FAO, 2001; Morato et al., 2006), and such a trend has also been observed in the Pacific of Latin America (Hilbourn et al., 2003; Pauly et al., 2005; Arana et al., 2009). The specific life-history characteristics of many deepwater organisms (e.g., longer life span, slow growth, late sexual maturity, low fecundity) make them especially vulnerable to depletion with a low capacity for recovery from overexploitation (Cheung et al., 2005; Morato et al., 2006). According to Polidoro et al. (2008), the lack of life history data of the exploited deepwater species is a major limitation for the development and implementation of adequate management measures.

The vast majority of the commercial fishing activities in Costa Rica are concentrated along the Pacific coast (Wehrtmann and Nielsen-Muñoz, 2009). Considering the Pacific deepwater shrimp fishery, the target species are *Heterocarpus affinis* Faxon, 1895, *H. vicarius* Faxon, 1895 and *Solenocera agassizii* Faxon, 1893 (Wehrtmann and Echeverría-Sáenz, 2007; Wehrtmann and Nielsen-Muñoz, 2009).

S. agassizii (locally called "camarón fidel") is distributed along the Pacific coast from Nicaragua to Peru. It prefers soft (mud and sandy-mud) bottoms and can be found at depths between 16 and 350 m (Holthuis, 1980; Hendrickx, 1995). Although there are three species of *Solenocera* Lucas, 1849 reported for Costa Rica (Vargas and Wehrtmann, 2009), *S. agassizii* is the only commercially exploited species of the genus, and represents up to 30% of the total shrimp landings of Costa Rica (Wehrtmann and Nielsen-Muñoz, 2009). Highest yearly landings were observed in 1986 with 2.6×10^6 kg. Subsequently, the landings dropped to values well below 0.5×10^6 kg, and recent data indicate a further reduction of *S. agassizii* landings to roughly 0.25×10^6 kg per year (Wehrtmann and Nielsen-Muñoz, 2009). Despite this alarming situation and the economical importance of this species, our knowledge about the biology of *S. agassizii* is rather limited. Most information focuses on the taxonomy (Holthuis, 1980; Hendrickx, 1995), and the reproductive biology of this solenocerid shrimp is completely unknown. Such a situation impedes any effort to develop an appropriate management plan for a sustainable exploitation of this resource.

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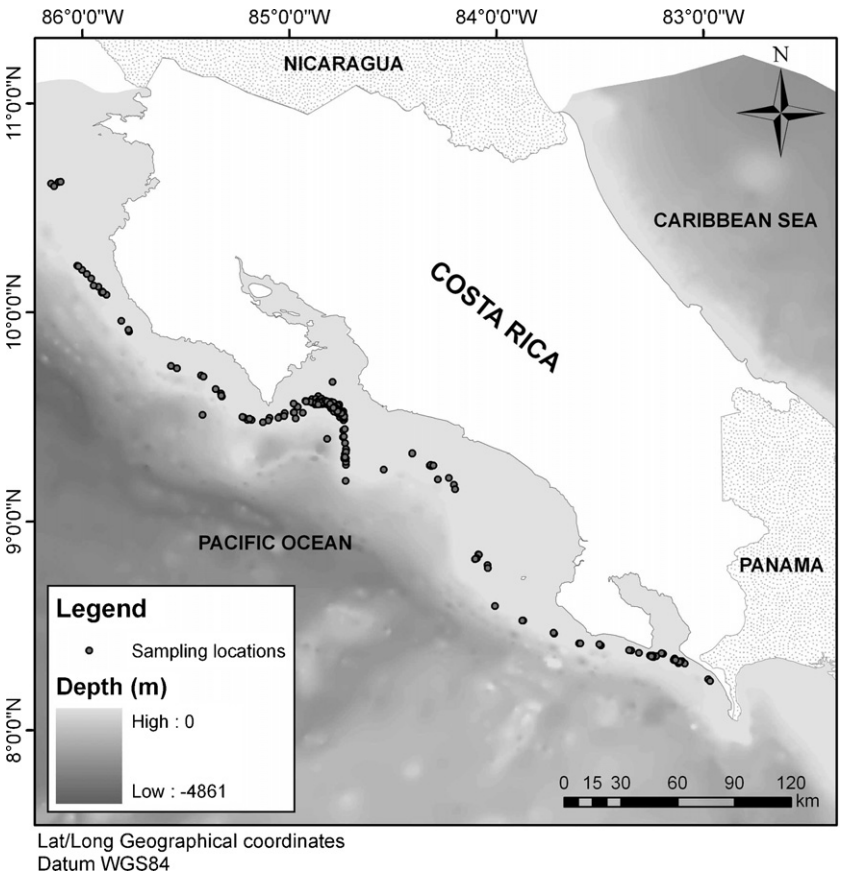

Fig. 1. Geographical distribution of sampling sites of *Solenocera agassizii* along the Pacific coast of Costa Rica. Samples were collected with commercial shrimp trawlers in the frame of a monthly monitoring program carried out between January 2007 and January 2008.

Adequate knowledge about the reproductive biology of the exploited species is one of the primary concerns in developing management tools for fishery science (Belcari et al., 2003; Branco, 2005; Carbonell et al., 2006; Castilho et al., 2007). The description of the gonad development in females of an economically important species is an essential element for assessing possible patterns in the reproductive cycle of a species (Levi and Vacchi, 1988; Castilho et al., 2007).

Thus, the aim of the present study was to classify the ovarian development of *S. agassizii* into easily recognizable stages, combining both microscopic and macroscopic features. The results of such a classification might be a useful and important tool for future monitoring programs of *S. agassizii*, which are essential for the urgently needed establishment of a proper management plan for a sustainable exploitation of this species.

2. Materials and methods

2.1. Survey locations and dates

Specimens of *S. agassizii* were collected between January 2007 and January 2008 at depths ranging from 150 to 195 m. These samples were obtained with commercial shrimp trawlers during a monthly monitoring program along the Pacific coast of Costa Rica (Wehrtmann and Nielsen-Muñoz, 2009). Fig. 1 indicates the locations where *S. agassizii* was collected for the present study.

2.2. Stage determination

Shrimps were sexed according to the presence (males) or absence (females) of the petasma (Hendrickx, 1995). Fresh females were fixed on board the shrimp trawler in a Davidson's solution for a period of 24–48 h (Bell and Lightner, 1988). For each female we measured the carapace length (CL: straight line from posterior edge of the eye orbit to the outer edge of the carapace), abdominal length (AL: from the first abdominal segment to the tip of the telson), and calculated total length (TL = CL + AL).

The females were dissected and their ovaries extracted. The following criteria were used to classify their developmental stages macroscopically: color, shape, size and position regarding the heart and the hepatopancreas. To validate these macroscopic developmental stages, portions of ovarian tissue were prepared for histological examination. In the laboratory the ovaries were dehydrated in an ascending ethanol series (80–100%), cleared in toluene, embedded in paraffin wax, and sectioned at 6 μm. Subsequently, ovary sections were stained with Delafield's haematoxylin and eosin (Bell and Lightner, 1988), and mounted in Clariol for microscopic examination. Maximum diameters of 30 oocytes per female were measured under the light microscope (Leica CME) using a total magnification of 400×. Only oocytes with a visible nucleus were measured.

The gonadosomatic index (GSI) was calculated according to the following equation: $OW/BW \times 100$, where *OW* (ovary weight) and *BW* (body weight) were obtained by drying them in an oven at 60 °C for 48 h. They were then weighed to the nearest 0.0001 (Sartorius TE 64).

2.3. Statistics

An ANCOVA (analysis of covariance) (Zar, 1999) was applied to test for significant differences between stages of ovarian development and both mean oocyte diameter and means of GSI, with TL

as the co-variable. An *a posteriori* Tukey test (Zar, 1999) was performed to establish possible differences between developmental stages.

3. Results

3.1. Stage description

The ovaries of *S. agassizii* consist of two lobes that are formed by four smaller lobes (three lateral and one frontal located in the carapace). In smaller females these four smaller lobes are not easily differentiated. In the first abdominal segment the lobes form two cylindrically shaped lobes that extend to the first portion of the telson. Based on the examination of 132 females, which ranged in size from 17.9 to 51.3 mm CL and from 55.5 and 148 mm TL, the following four ovarian developmental stages were identified utilizing macroscopic and microscopic criteria.

3.1.1. Stage I: immature

In the cephalothorax, the ovary has a pale white color as it reaches its most frontal position close to the heart. In the abdomen, the ovary splits into two parallel thin and translucent lobes, through which the intestinal tube can easily be seen (Fig. 2E). In fresh shrimps, the ovary cannot be seen through the exoskeleton. Histologically, this stage is composed principally of two basophilic cells: oogonia and small oocytes (also present in the subsequent stages). The oogonia are positioned centrally in each lobe, whereas the small oocytes make-up most of the tissue and can be found in the entire ovary. The small oocytes are rounded cells with a mean diameter of 56.2 ± 14.50 μm, varying between 40 and 85 μm and a coefficient of variance (CV) of 25.8%. These cells are characterized by a barely visible cytoplasm and a large nucleus with three to five nucleoli at their periphery (Fig. 2A). The GSI-values obtained for this stage varied between 0.15 and 0.58%, with a mean of 0.36% (±0.150, CV: 41.6%).

3.1.2. Stage II: previtellogenic

The ovary is thin and has a slightly pink color, losing its translucidity in the cephalothorax; it surpasses the position of the heart and reaches the hepatopancreas (Fig. 2F). The intestine can barely be seen in fresh shrimp. Histologically, in this stage three types of cells were present: follicular, oogonia and previtellogenic oocytes (basophilic) (Fig. 2B). The previtellogenic oocytes represent more than 50% of the cell composition and are substantially larger than the small oocytes found in stage I (mean 128.9 ± 9.20 μm, varying between 116 and 140 μm, CV: 7.1%). The values of GSI varied between 0.30 and 1.13%, with a mean of 0.72% (±0.210, CV: 29.17%).

3.1.3. Stage III: vitellogenic

In earlier phases of this stage, the ovary is pinkish or orange, and as it develops toward Stage IV it turns into a dark burgundy color. In fresh shrimps changes in both ovary coloration and width allow its observation through the exoskeleton. In a dissected shrimp it is impossible to observe the intestinal tube through the ovary due to the opacity of the latter (Fig. 2G). Fig. 2G illustrates an ovary in transition from stage II to stage III. The ovary surpasses the position of both the heart and the hepatopancreas. Histologically, three cell types are present: follicular, oogonia and vitellogenic oocytes (acidophilic) (Fig. 2C) with vitellogenic oocytes representing more than 70% of the volume of the ovary. Unlike previtellogenic oocytes, vitellogenic oocytes contain yolk globules (acidophilic) and have a larger diameter (mean 182.0 ± 30.30 μm, CV: 16.6%). The germinal zone is reduced but in the same location as in Stage II, whereas previtellogenic oocytes can be found throughout the ovary. The GSI values fluctuated between 1.07 and 10.19%, with a mean of 3.79 ± 2.51% and a CV of 66.20%.

3.1.4. Stage IV: mature

The width of the ovary is similar to that in stage III, but it occupies more space in the cephalothorax, passing the heart and hepatopancreas region, and reaching the ocular orbits (Fig. 2H). The dark burgundy colored ovary covers the intestinal tube and can be observed in fresh females through the exoskeleton. A distinction between Stage III and Stage IV in fresh shrimp is not possible through the exoeskeleton. Histologically two cell types are present: oogonia and vitellogenic oocytes with cortical rods. Since they represent more than 70% of the ovary's volume, the cortical rods present below the membrane of the vitellogenic oocytes (Fig. 2D) allow this stage to be distinguished from earlier ones. The vitellogenic oocytes have a mean diameter of 255.4 ± 16.50 μm, and a CV of 6.5%. The GSI values varied between 2.95 and 12.96%, with a mean of 6.65% (±2.780 CV = 41.80%).

The mean diameter of oocytes differed significantly between all stages of ovary development (ANCOVA, $P < 0.05$; Tukey, $P < 0.05$), independent of the TL of the females. Similarly, mean GSI increased significantly with the stage of ovarian development (ANOVA; $f = 85{,}697$, $P < 0.001$). Regarding the GSI means, there were significant differences between all ovarian developmental stages (Tukey, $P < 0.05$), except between Stage I and II (Tukey, $P > 0.05$). Both the GSI and the diameter of oocytes increased with ovarian development (Table 1).

4. Discussion

Here we describe four ovary developmental stages for the females of *S. agassizii*. The number of stages mentioned for other penaeoidean shrimps as *Farfantepenaeus paulensis* (Peixoto et al., 2003); *Aristeus antennatus* (Carbonell et al., 2006); *Trachysalambria curvirostris* (Yamada et al., 2007) varies typically between four and six stages, which coincide generally with the macroscopic and histologic characteristics described herein for *S. agassizii*. The principal phases of ovary development represent (1) immature or undeveloped, (2) developing or previtellogenic, (3) vitellogenic or nearly ripe, (4) mature or ripe, and (5) reabsorbing ovaries (Ohtomi et al., 1998; Ayub and Ahmed, 2002; Dumont et al., 2007). In the specimens examined by us, we did not detect a fifth developmental stage (reabsorbing ovaries). This situation may be related to the fact that this stage has a duration of only a few days (Baelde, 1992), which makes it more difficult to find females in this stage (Dumont and Dĭlncao, 2004). Moreover, reabsorbing ovaries are difficult to differentiate from early stages of development (Baelde, 1992; Ohtomi et al., 1998; Peixoto et al., 2003, 2005; Dumont et al., 2007).

We cannot exclude the possibility of the existence of a fifth developmental stage in *S. agassizii*, and the examination of additional material may reveal the presence of reabsorbing ovaries. However, even the current description of four ovarian developmental stages will facilitate future assessment of the reproductive periodicity of *S. agassizii*.

The presence of centrally located germinal cells and highly basophilic oogonia at the periphery of the ovaries is associated with a slim and translucid ovary in Stage I (Fig. 2A and E). Similar observations have been reported from other shrimp species as *Solenocera melantho* (Ohtomi et al., 1998), *Penaeus brasiliensis* (Quintero and García, 1998), *A. antennatus* (Demestre and Fortuno, 1992; Carbonell et al., 2006).

The central position of the germinal cells (proliferation zone) throughout the ovary development, as observed in *S. agassizii*, seems to be a common feature among penaeiodean shrimp species (*Artemisa longinaris*: Dumont and Dĭlncao, 2004; *F. paulensis*:

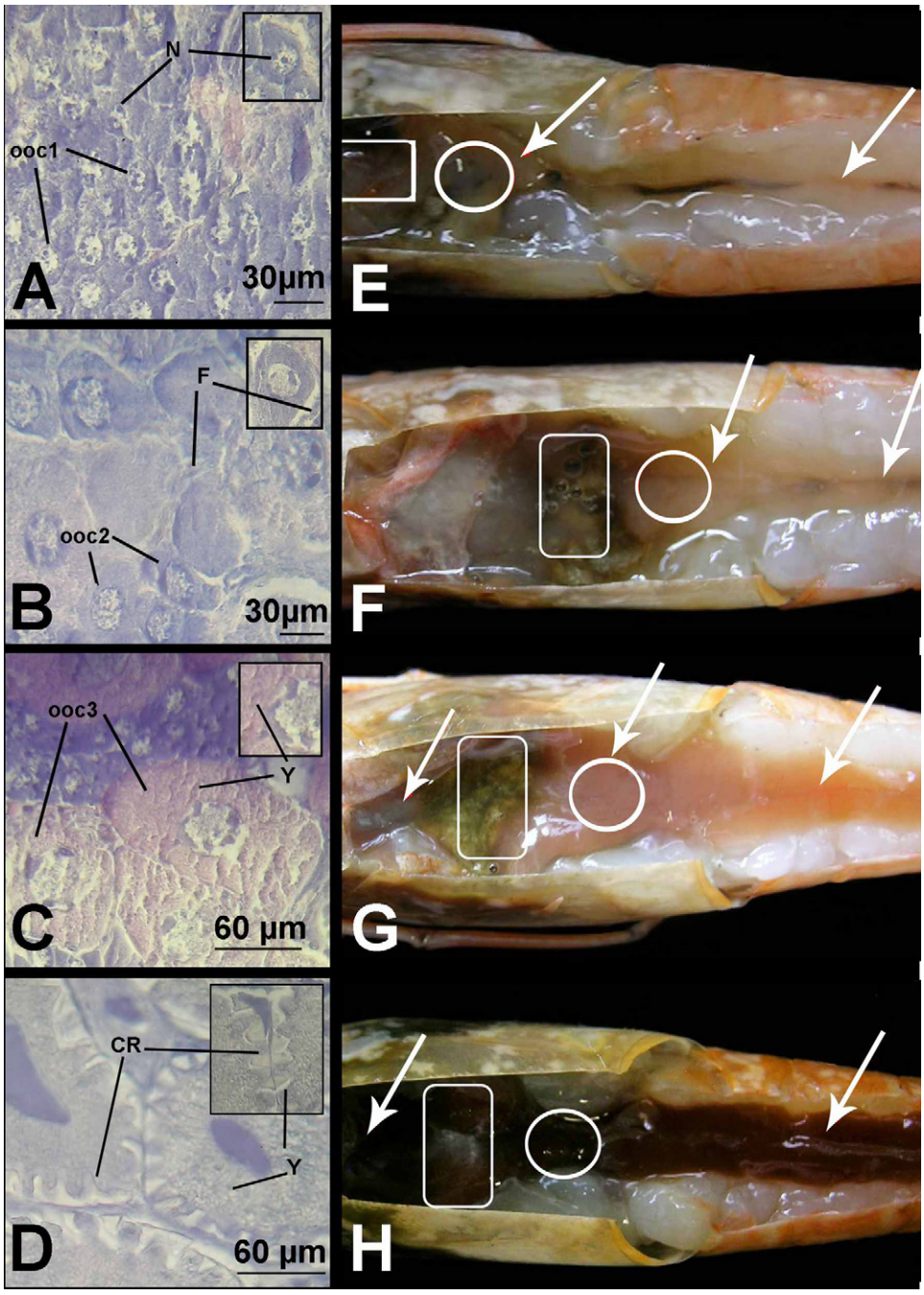

Fig. 2. Ovary development of female *Solenocera agassizii*. Microscopic developmental stages, with hematoxilin-eosin staining technique (A–D): Stage I (A), small oocytes (ooc1) with nucleoli (N) in the nucleus. Box: magnified oocytes with nucleoli. Stage II (B), previtellogenic oocytes (ooc2). Box: magnified previtellogenic oocytes and follicular cells (F). Stage III (C), vitellogenic oocytes (ooc3) with yolk globules (Y) in ooplasma. Box: yolk globules magnified. Stage IV (D), vitellogenic oocytes with cortical rods (CR) on its periphery. Box: cortical rods magnified. Macroscopic developmental stages (E–H): Stage I (E), very thin and translucent ovaries that barely surpass the position of the heart. Stage II (F), pink ovary, thicker than in stage I, touches the position of the hepatopancreas. Stage III (G), from orange to burgundy colored thick ovary that surpasses the position of hepatopancreas. Stage IV (H), dark wine coloration; the ovary surpasses the position of hepatopancreas. The arrows indicate the position of the ovary in the abdomen and cephalothorax. The circle indicates the position of the heart; the box that of the hepatopancreas. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

Peixoto et al., 2003). According to Carbonell et al. (2006), such a positioning of the germinal cells may be the result of the pressure inflicted by growing oocytes.

The development of previtellogenic oocytes and the appearance of the surrounding follicular cells associated with the loss of translucity at a macroscopic level characterize the start of the endogenous vitellogenesis phase (Baelde, 1992; Quinitio et al., 1993; Anderson et al., 1984, 1985; Ohtomi et al., 1998; Carbonell et al., 2006; Yamada et al., 2007; Dineshbabu and Manissery, 2008). In this phase, follicular cells have been described as necessary for material entrance from the oolema to the cells during exogenous vitellogenesis (*F. paulensis*: Peixoto et al., 2003; *A. antennatus*: Carbonell et al., 2006). This information coincides with the microscopic appearance of follicular cells around the oocytes in Stage II (previtellogenic phase, Fig. 2B) together with a macroscopic loss of translucity (Fig. 2F) in the ovaries of female *S. agassizii*.

During the exogenous vitellogenesis, there is a massive development of yolk plateles in previtellogenic oocytes, which transforms

Table 1
Macroscopic and microscopic characteristics of each of the four stages of ovarian development in *Solenocera agassizii*.

Stage	GSI		Oocyte diameter		Main cellular type (microscopic)	Macroscopic characteristics
	($x \pm$ SD) (n)	CV (%)	($x \pm$ SD μm) (n)	CV (%)		
I	0.36 ± 0.150[a] (14)	41.6	56.2 ± 14.50 (33)	25.8	Oogonia	NV; translucid to white; reaches heart position
II	0.72 ± 0.210[a] (8)	29.7	128.9 ± 9.20 (28)	7.1	Previtellogenic oocyte, follicular cells	NV; white to pink; surpasses heart position
III	3.79 ± 2.510 (9)	66.2	182.0 ± 30.30 (15)	16.6	Vitellogenic oocyte	V; pink to orange; surpasses heart and hepatopancreas position
IV	6.65 ± 2.780 (10)	41.8	255.4 ± 16.50 (15)	6.5	Cortical rods	V; burgundy to brown; surpasses heart and hepatopancreas position

(n): number of females analyzed for GSI or oocyte diameter.
CV: coefficient of variance (SD/x)
NV: gonad not visible through the exoskeleton of fresh shrimp.
V: gonad visible through the exoskeleton of fresh shrimp.
[a] No significant differences between stages.

Table 2
Stages of ovarian development described for different penaeoid shrimps.

Species (number of stages)	Gonad development stages	Reference (study zone)
Aristeidae		
Aristeus antennatus (Risso, 1816) (6)	Type I: immature juvenile Type II: resting adult stage Type III: folliculogenesis Type IV: exogenous vitellogenesis Type V: mature ovary, spawning adult Type VI: post-spawn ovary, absorbing	Carbonell et al. (2006) (northwestern Mediterranean Sea)
Penaeidae		
Farfantepenaeus paulensis Pérez-Farfante, 1967 (4)	Stage I (immature) Stage II (developing) Stage III (mature) Stage IV (evacuated)	Peixoto et al. (2003) (southern Brazil, 27°S)
Farfantepenaeus paulensis Pérez-Farfante, 1967 (4)	Stage I (immature) Stage II (developing) Stage III (mature) Stage IV (evacuated)	Dumont et al. (2007) (northern coast of Santa Catarina State, Brazil)
Fenneropenaeus (Penaeus) penicillatus (Alcock, 1905) *Fenneropenaeus (Penaeus) merguiensis* (De Man, 1888) *Metapenaeus affinis* (Milne Edwards, 1837) *Penaeus stylifera* (Milne Edwards, 1837) (6)	1. Non-developed ovary 2. Developing ovary 3. Almost mature ovary 4. Totally mature ovary R. Reabsorbing ovary R/D. Reabsorbing/developing ovary	Ayub and Ahmed (2002) (coast of Pakistan)
Trachysalambria curvirostris (Stimpson, 1860) (4)	Stage 1: oogonium and synapses Stage 2: early perinucleoli, late perinucleoli without yolk Stage 3: late perinucleoli, with and without yolk Stage 4: prematuration	Yamada et al. (2007) (Tokyo Bay, Japan)
Solenoceridae		
Haliporoides sibogae (De Man, 1907) (4)	1. Previtellogenic stage (germinal cells predominant) 2. Previtellogenic stage (oocytes predominant) 3. Vitellogenic stage 4. Postvitellogenic stage	Baelde (1992) (southeastern Australia)
Solenocera agassizii Faxon, 1893 (4)	1. Immature 2. Previtellogenic 3. Vitellogenic 4. Mature	Present study (Pacific coast, Costa Rica)
Solenocera melantho de Man, 1907 (4)	1. Proliferation 2. Previtellogenic 3. Vitellogenic 4. Prematuration	Ohtomi et al. (1998) (Kagoshima Bay, Japan)

these oocytes into vitellogenic oocytes. At the same time, the ovary acquires greater macroscopic dimensions and loses its translucity (*F. paulensis*: Peixoto et al., 2003; *A. antennatus*: Carbonell et al., 2006). Conspicuous yolk granules can be observed in the cytoplasm of the oocytes of *S. agassizii*, the same as the increase in volume and loss of translucity can be easily observed in stage III (Fig. 2C and G).

The appearance of cortical crypts, the notable reduction in nucleous diameter due to the germinal vesicle breakdown (GVBD; Anderson et al., 1984, 1985), and the disappearance of the follicu-

lar cells characterize mature oocytes (Peixoto et al., 2003; Carbonell et al., 2006; Dumont et al., 2007). According to Clark et al. (1980, 1990, 1994), the cortical crypts prepare the oocytes for a possible fertilization whereas the disappearance of follicular cells indicates that spawning will occur in less than eight days. Anderson et al. (1984, 1985) indicated that the spawning in *Sicyonia ingentis* is characterized by the loss of the folicullar cell matrix, which will liberate the oocytes in the ovaric lumen. These characteristics were also observed in females of *S. agassizii* with ovaries in Stage IV (Fig. 2D). Therefore, it seems safe to assume that females in this stage will soon be ready to release their oocytes.

The macroscopic differentiation (ovary coloration and size) of the four stages of ovary development can be carried out in dissected females of *S. agassizii*. Based on the possibility of observing the ovary through the exoskeleton in fresh specimens, females can be grouped in NV (not visible) (Stages I and II) and V (visible) (Stages III and IV) (Table 1). The use of an ovary classification through dissection is a common and useful strategy applied to monitoring programs for many commercially important shrimp species (Palacios et al., 1993, 2003; Alvaro and Dupré, 2000; Leal-Gaxiola et al., 2001). On the other hand, the possibility of a classification without the need to dissect the shrimps represents an important tool for a simple and rapid assessment of ovary development in the field (Levi and Vacchi, 1988).

The following results support the determination of four distinct ovary stages, which can be used as reliable indicators of stage maturity of female *S. agassizii*: (1) CV values in Table 1, which indicate low variance for the GSI and oocyte diameters for each stage; (2) significant differences in the mean diameter of oocytes in each stage independent of the female size (Table 1), which indicate an increase in oocyte diameters with stage development and (3) the GSI results (Table 1), which indicate an increase in gonad weight with stage development (Tables 1 and 2).

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