

Reproductive cycle and gonadal development of *Leukoma pectorina* (Bivalvia: Veneridae) on the northern coast of Brazil

Ewertton Souza Gadelha ¹, Ricarla Romilia Viana dos Santos ², Rosália Furtado Cutrim Souza ³

¹Emílio Goeldi Paraense Museum, Tancredo Neves Avenue, 1901, Montese, 66077-830, Belém, Pará, Brazil.
(ESG) (Corresponding author) E-mail: ewerttoo@yahoo.com.br ORCID iD: <https://orcid.org/0000-0002-5741-6547>

²Work Cooperative of Agricultural Professionals of the State of Pará, Brazil.
(RRVS) E-mail: engricarlaviana@gmail.com ORCID iD: <https://orcid.org/0000-0003-2456-8226>

³Federal Rural University of the Amazon, Avenida Tancredo Neves, 2501, Montese, 66077-830, Belém, Pará, Brazil.
(RFCS) E-mail: rosalia.souza@ufra.edu.br ORCID iD: <https://orcid.org/0000-0002-2843-7760>

Summary: The reproductive cycle and gonadal development of the “sarnambi”, *Leukoma pectorina* (Lamarck, 1818), was studied between June 2008 and July 2009 on the coast of Pará (Brazil). Histological analyses were performed on 633 individuals and, through microscopic observations, sexing and characterization of gonadal development were carried out. Subsequently, based on histological images, the diameters of oocytes were counted and measured to determine the reproductive period. The population showed a sex ratio of 1:1.3 (female: male). Females were significantly more frequent in small sizes of 2–7 mm, while larger individuals predominantly consisted of males. The size of the first maturation occurred at 11.80 mm for males and 14.40 mm for females. The population exhibited continuous spawning, with abundance of oocytes correlating with salinity. It is concluded that there are five stages of gonadal development and gonochorism, a typical strategy of tropical bivalves, supporting global hypotheses. For the preservation of the species, it is recommended that these organisms be captured with shell lengths above 15 mm. In addition, further research on the parasite found in this study is necessary, as it could compromise the population’s fecundity rate.

Keywords: mollusc; fishery resource; reproduction; gametogenesis; bivalves; size at first maturity

Ciclo reproductivo y desarrollo gonadal de *Leukoma pectorina* (Bivalvia: Veneridae) en la costa norte de Brasil

Resumen: Se estudió el ciclo reproductivo y el desarrollo gonadal del “sarnambi”, *Leukoma pectorina* (Lamarck, 1818), entre junio de 2008 y julio de 2009 en la costa de Pará (Brasil). Se realizaron análisis histológicos en 633 individuos y, a través de observaciones microscópicas, se determinó el sexo y se caracterizó el desarrollo gonadal. Posteriormente, con base en imágenes histológicas, se contaron y midieron los diámetros de los ovocitos para determinar el período reproductivo. La población presentó una proporción de sexos de 1:1.3 (hembra: macho). Las hembras fueron significativamente más frecuentes en los tamaños pequeños de 2-7 mm, mientras que los individuos más grandes consistieron predominantemente en machos. El tamaño de la primera maduración fue de 11.80 mm para los machos y 14.40 mm para las hembras. La población presentó desove continuo, con la abundancia de ovocitos correlacionándose con la salinidad. Se concluye que existen cinco etapas de desarrollo gonadal y que los organismos son gonocóricos, adoptando una estrategia típica de los bivalvos tropicales, lo que respalda hipótesis globales. Para la conservación de la especie, se recomienda que estos organismos sean capturados con longitudes de concha superiores a 15 mm. Se requiere más investigación sobre el parásito encontrado en este estudio, ya que podría comprometer la tasa de fecundidad de la población.

Palabras clave: molusco; recurso pesquero; reproducción; gametogénesis; bivalvos; tamaño de la primera madurez.

Citation/Como citar este artículo: Gadelha E.S., Santos R.R.V. dos, Souza R.F.C. 2025 Reproductive cycle and gonadal development of *Leukoma pectorina* (Bivalvia: Veneridae) on the northern coast of Brazil. Sci. Mar. 89(2): e098. <https://doi.org/10.3989/scimar.05532.098>

Editor: E. Galimany.

Received: April 10, 2024. **Accepted:** January 29, 2025. **Published:** August, 26, 2025.

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INTRODUCTION

The artisanal exploitation of benthic organisms is of great socio-economic importance to Latin American countries and is a significant source of income and subsistence for traditional communities in the coastal zone (Castilla and Defeo 2001). On the Brazilian coast, various species of bivalves are caught rudimentarily by traditional communities without any management measures.

On the northern coast of Brazil, Beasley et al. (2005) reported that bivalves are commercially exploited by riverside populations on Ajuruteua beach in Bragança. According to Borcem et al. (2011), in the local communities of the municipality of Marapanim in the state of Pará, the capture of the bivalve *Leukoma pectorina* (Lamarck, 1818) generates income and subsistence for the local population.

The species *L. pectorina*, popularly known as “sarnambi”, belongs to the family Veneridae Rafinesque, 1815, and is distributed in the lower Caribbean, from Suriname to Brazil, inhabiting intertidal to infralittoral zones on sand-muddy or muddy beaches (Denadai et al. 2006, Rios 2009). The distinctive characteristics of this species compared with other Venerids are its rounded shell shape and the presence of a shield only on the left valve (Amaral et al. 2005). On Algodoad-Maiandeuá Island, along the Amazon coast of Brazil, this organism is predominantly harvested by women. The sarnambis are prepared within the household, and most of the catch is sold to local commercial establishments. The fishing of this bivalve is a sporadic activity used to complement family income, and it is more common during the dry season when tourism increases and organism density is higher (Silva et al. 2012). Knowledge about the reproductive biology of the species still has many gaps; the literature only cites works on functional anatomy (Guerón and Narchi 2000) and sperm ultrastructure (Matos et al. 1997).

Due to the extractive exploitation of these bivalves throughout the year, increasing environmental degradation and the scarcity of studies on their reproductive dynamics, the adoption of management measures is limited, causing various problems for natural clam beds in various coastal regions and jeopardizing the renewal of these stocks (Munro 1979, Matics 1997). Reproductive data on bivalves is essential for developing appropriate fishery management: for example, size at first maturity is one of the parameters commonly evaluated to assess the management of fish and shellfish stocks, allowing for the renewal of stocks and avoiding overfishing (Tirado et al. 2002, Williams and Babcock 2005, Nunes et al. 2020).

The reproductive cycle in bivalves involves gonadal development, gamete maturation and spawning, with significant variation in the timing and duration of each stage both within and between species (Gosling 2003). This is due to the influence of exogenous factors (mainly temperature, salinity and rain) that are involved in the reproduction processes that the organism is undergoing, which play an important role in spawning synchronization (Seed 1976). Due to this influence of the environment on the reproductive cycle, reproduction hypotheses predict that marine invertebrates have a limited reproductive period in polar regions and a longer period in tropical regions (Giese 1959, Defeo and Cardoso 2002). Therefore, this study aims to describe and analyse the reproductive cycle and gonadal development and estimate the size at first maturity of *L. pectorina* on the northern Brazilian coast. Thus, this paper contributes scientific knowledge regarding the biology of the sarnambi, serving as an important resource to aid in the management of its exploitation. The aim is to prevent overfishing and, consequently, avoid negative social and economic impacts, considering that traditional populations in Marapanim rely on this fishery resource as a source of income.

MATERIAL AND METHODS

Study area and sampling

This study was carried out in the municipality of Marapanim belonging to the Salgado micro-region, which is part of the Northeast Pará mesoregion in the North of Brazil (Fig. 1), which has a tropical rainy climate (up to 3000 mm per year), an average air temperature of 27.7°C and humid conditions (humidity between 80% and 85%), and is subject to semidiurnal macro-tides (up to 5 m, Furtado 1978, Berrêdo et al. 2008). The region is influenced by the Intertropical Convergence Zone, which determines the highest rainfall between January and June and the lowest rainfall between July and December. Rainfall varies from 10.4 mm in August to 760.6 mm in February (Furtado 1978, Berrêdo et al. 2008, Sepof 2013). The lowest salinity values recorded occur during the rainy season. The minimum salinity occurs in March and the maximum in October (Berrêdo et al. 2008).

Sampling was carried out monthly from June 2008 to July 2009 (except July 2008 and June 2009) at syzygy low tide on a natural bed located on the right side of the Furo Camará, on the fishing village beach (00°35'35.40"S 047°41'26.60"W) in the state of Pará (Fig. 1).

Individuals were randomly collected monthly along the beach using a scarifier. There was no standardization of the number of individuals throughout the collections. The anteroposterior length was then measured using a 0.1 mm caliper, ranging from 2.2 to 39.1 mm (20.64±9.89).

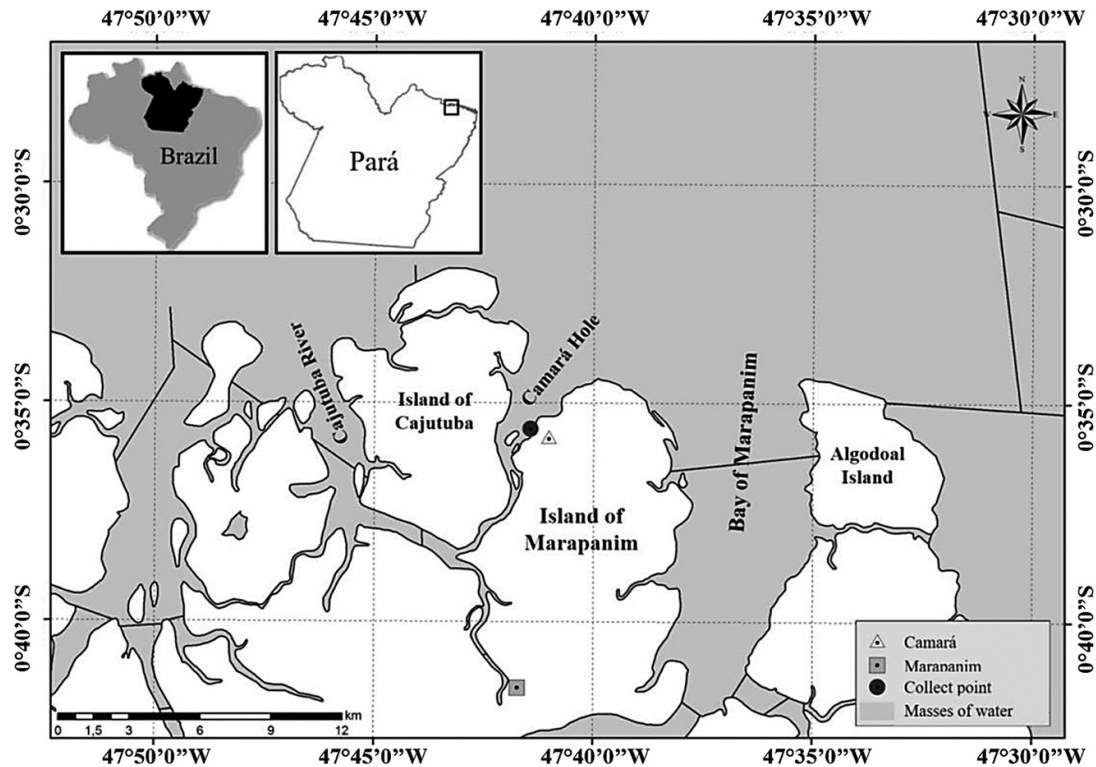


Fig. 1. – Map of the study area with the sampling point.

Histological analysis

In the laboratory, we removed the visceral mass from the shell and immersed it in Davidson's solution for 24 hours. Afterward, we extracted the gills, labial palps, and mantle edge, transferring the gonad to 70% alcohol. The histological method modified from Junqueira and Junqueira (1983) was used: the gonads were processed with the paraffin technique, sectioned into 5 µm thick slices and stained with haematoxylin-eosin (HE).

The histological preparations of the gonadal sections were examined using a binocular microscope. The gonads were classified into five stages (I, immature; II, in maturation; III, ripe; IV, spawning; V, cytotoxicity) following previous studies in bivalves (Narchi 1976, Herrmann et al. 2009a). Photomicrographs of histological sections were captured using Motic Image Plus 2.0 to determine the oocyte number and average oocyte diameter following the methodology described by Herrmann et al. (2009a) and Gadelha et al. (2019), using Image Tool 3.0 software. The gonad image (only for females) was sectioned into a 1 mm² area, and the oocytes within this area were counted.

Size at first maturity

Length at first maturity (L_{50}) indicates the size at which 50% of the population reaches sexual maturity. The proportion data from 633 individuals (stage II: maturing; stage III: mature; stage IV: spawning; and stage V: cytotoxicity) were estimated using the SizeMat package (Torrejon-Magallanes 2020) available in the R software (R Core Team, 2022). The function to be used to estimate gonadal maturity is "gonad_mature". This function uses the logistic (GLM) approach:

$$P = \frac{1}{1 + e^{-(a+b \cdot L)}}$$

where P is the probability of an individual being mature at a particular size, a is the intercept, b is the angular coefficient and L is the shell length (Pereira et al. 2024).

Environmental variables

Surface seawater temperature and surface salinity were obtained from field samplings. Additionally, monthly precipitation data were obtained from <https://portal.inmet.gov.br/>.

Statistical analyses

The sexual difference between females and males was tested using the χ^2 (chi-square) test for $\chi^2=0.05$ and $df=1$. To reduce the error of the chi-square with 1 df we made the adjustment proposed by Yates (1934). To detect the difference between the dry and rainy periods, we applied the nonparametric Mann-Whitney (U) test to the data on environmental variables, oocyte abundance, oocyte diameter and the stages mature and in elimination. Spearman correlation and the generalized linear model (GLM) were used to examine the relationships between oocyte abundance, mature and spawning stages, and the explanatory variables (salinity and precipitation); due to low variance, temperature was not included in the modelling. The GLM was built using a Gaussian model identity link function. The Akaike information criterion (AIC) (Akaike 1973) was used to compare the models, with lower values indicating a more parsimonious model than one fitted with a higher AIC. We used the R platform (R Core Team, 2014) to generate the GLM using the nlme package, the gls function, and the “ML” maximum likelihood estimation method. Mann-Whitney and chi-square tests were performed with the PAST software, version 3.02 (Hammer et al. 2001).

RESULTS

Environmental variables

During the study period, the surface seawater temperature ranged monthly from 28°C to 29°C, and salinity from 4 (May/2009) to 36 (October/2008), while rainfall had the widest range, from 0 mm to 412 mm (Fig. 2).

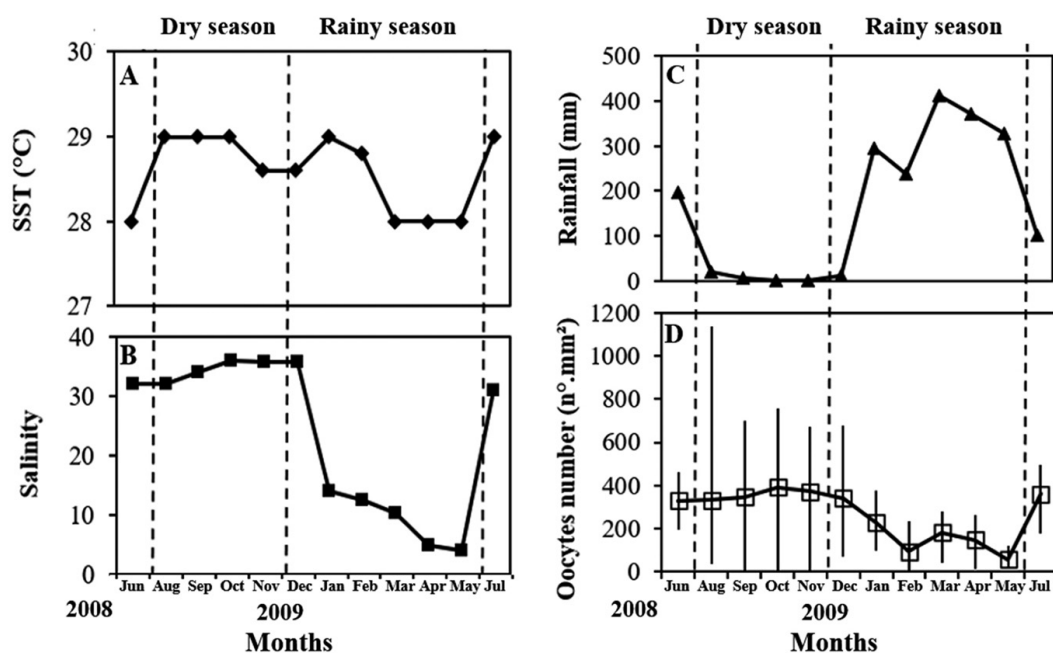


Fig. 2. – Variation in environmental parameters and biological data between June 2008 and July 2009. A, sea surface temperature (SST, °C); B, salinity (ppm); C, rainfall (mm); D, average oocyte abundance (oocytes mm⁻²).

Sex ratio

During the study period, 633 individuals were analysed, of which 272 were females (43%) and 361 were males (57%). Detailed numbers by size range of sampled bivalves are shown in Table 1. There was a significant global predominance of males ($\chi^2=12.8$, $p<0.05$), with a sex ratio of 1 F:1.3 M. On a monthly basis, males were predominant only in January 2009 and April 2009 ($\chi^2=5.56$; $\chi^2=4.5$, $p<0.05$, respectively). For the observations by class interval, females were more frequent in the 2–7 mm interval ($\chi^2=14.73$, $p<0.05$), with a sex ratio of 10F:1M, while

males had a significant predominance in the 27–32 mm and 32–37 mm intervals, with a sex ratio of 1F:1.7M and 1F:2.2M, respectively (Fig. 3).

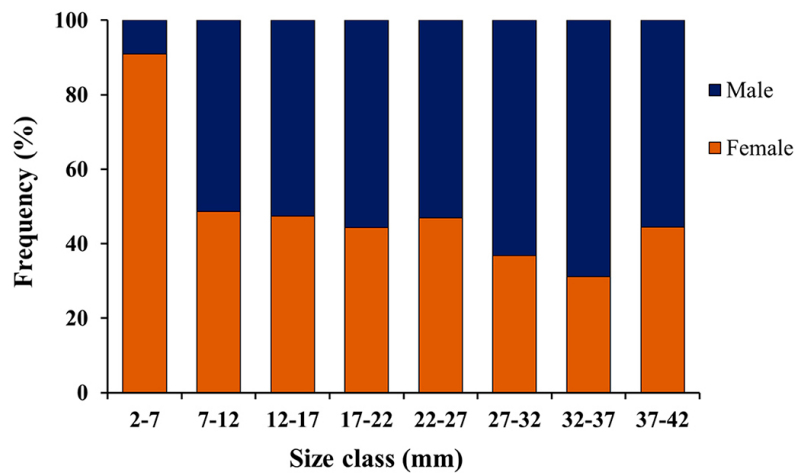


Fig. 3. – Size class distribution of males and females of *Leukoma pectorina*.

Table 1. – Number and length range (mm) of samples collected for histological analysis.

Range length (mm)	Females	Males	Total
2–7	20	2	22
7–12	17	18	35
12–17	37	41	78
17–22	54	68	122
22–27	54	61	115
27–32	49	84	133
32–37	37	82	119
37–42	4	5	9
Total	272	361	633

Gonadal development stages

Based on the microscopic visualizations of the gonadal structures, we described and classified five stages of gonadal development of males and females of *L. pectorina*: immature (I), in maturation (II), ripe (III), spawning (IV), and cytolysis (V) (Fig. 4).

In females, the immature stage was characterized by the formation of ovarian follicles, with a high frequency of nests of mother cells adhered to the follicle wall and a low frequency of basophilic oocytes and cells in pre-vitellogenesis (Fig. 4A). While the in maturation stage simultaneously showed several phases of germ cells, with a predominance of cells in pre-vitellogenesis, vitellogenesis and basophilic oocytes, mature cells were not always present or when they were, they were located close to the follicle wall and in very small numbers; the follicle wall was thick with the presence of interfollicular tissue (Fig. 4B). In the ripe stage, we continued to see different phases of germ cells, but they differed from the previous stage in that there was a high frequency of mature oocytes and the follicles were large in diameter with the follicle wall distended, thin and juxtaposed due to the high quantity of oocytes inside the follicles (Fig. 4C).

In the spawning stage, the follicle wall was still distended, with part of it disappearing. There was an increase in interfollicular tissue, and we observed cells in the pre-vitellogenesis, vitellogenesis and mature stages, all three in reduced numbers, leaving spaces inside the ovarian follicles, which were sometimes occupied by loose connective tissue (Fig. 4D). However, the cytolysis stage had a thick follicle wall, the ovarian follicles were empty or had few mature oocytes, and nests of mother cells and some basophilic cells could be seen, as well as interfollicular tissue and loose connective tissue (Fig. 4E).

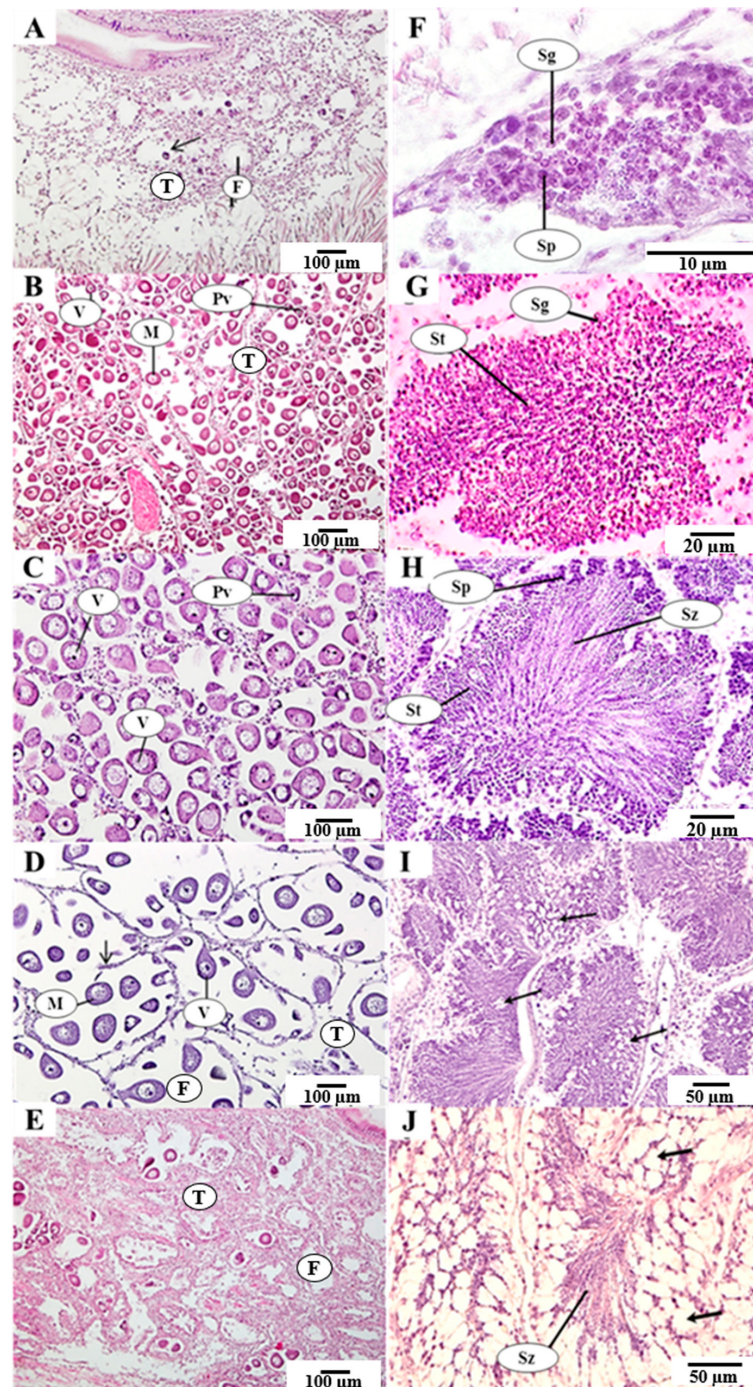


Fig. 4. – Photomicrographs of the gonadal development stages in *Leukoma pectorina*. A, immature female; B, female in maturation; C, ripe female; D, spawning female; E, female in cytolysis; F, immature male; G, male in maturation; H, ripe male; I, spawning male; J, male in cytolysis; PV, previtellogenic oocytes; V, vitellogenic oocytes; M, mature oocytes; F, ovarian follicle; T, interfollicular tissue; Sz, spermatozoa; Sp, spermatocyte; St, spermatid. The arrows indicate empty spaces with the release of mature gametes.

In males, the immature stage was characterized by having only stem cells and the beginning of the formation of the testicular tubules, with a low frequency of spermatogonia and spermatocytes (Fig. 4F). In the maturation stage, large numbers of germ cells were present in the spermatogonia, spermatid and spermatocyte stages, with complete formation of the testicular tubules, while the spermatozoa, when present, were few and scattered throughout the testicular lumen (Fig. 4G). In the ripe stage, there was an intensification of gametogenic phenomena, all the germ cell phases were observed, and unlike in the previous stage there was a predominance of organized spermatozoa in

the centre of the testicular tubules, between which there were no bundles of loose connective tissue. The testicular tubules were large in diameter with little space between them (Fig. 4H).

In the spawning stage, empty spaces could be seen inside the testicular tubule, as the spermatozoa were being expelled, but in some areas of the testicle there were still spermatocytes and spermatids. The diameter of the tubules began to decrease, and the follicle wall disappeared, leaving empty spaces where loose connective tissue was beginning to proliferate (Fig. 4I). In the cytolysis stage, most of the sperm cells were expelled from the testicular tubules, with interfollicular tissue containing stem or squamous cells observed. The walls of the tubules were significantly reduced, with proliferation of loose connective tissue (Fig. 4J).

Size at sexual maturity

According to the logistic equation method, the length of first sexual maturation was 11.80 mm for males and 14.40 mm for females. When the sexes were grouped, the population was estimated to reproduce at a size of 13.30 mm. The logistic curve indicating the first maturation size of *L. pectorina* can be seen in Figure 5.

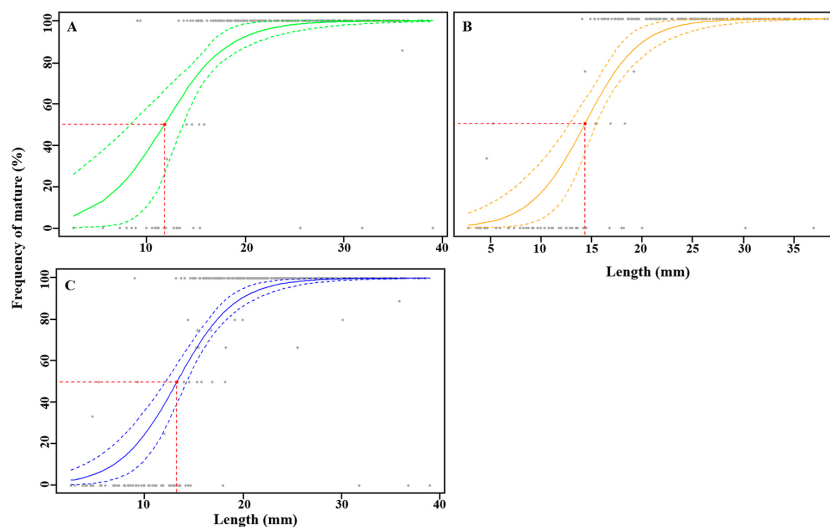


Fig. 5. – Logistic curve indicating the sexual maturity size of *L. pectorina*. A, red for males; B, orange for females; C, blue for sex grouped.

Reproductive cycle

The presence of all gonadal stages was observed every month during the study period in the histological analyses. This suggests that *L. pectorina* has continuous reproduction throughout the year. During the study period (except for May 2009) both sexes had individuals in the spawning stage, indicating continuous breeding. The highest frequency of individuals in this stage occurred from January to April 2009, coinciding with the rainy season. May 2009 showed a high frequency of individuals in gonadal maturation, marking a month of gonadal recovery after months of gametogenic release (Fig. 6).

Ripe females were not observed in November 2008, February 2009, April 2009 and May 2009. The highest frequency of mature males was in the months of June 2008 to September 2008 and July 2009, and that of mature females in the months of August 2008, December 2008 and January 2009. Spearman's correlation revealed that salinity and precipitation were not related to the frequency of mature individuals ($r_s=0.49$ $p=0.13$; $r_s=-0.45$ $p=0.13$, respectively) and spawning ($r_s=-0.03$ $p=0.9$; $r_s=0.11$ $p=0.71$, respectively).

Spearman's correlation revealed a positive relationship between salinity and oocyte abundance ($r_s=0.89$, $p=0.009$), with the same pattern demonstrated by the GLM model ($p=0.04$, Table 2). Conversely, rainfall showed a negative relationship with oocyte abundance according to Spearman's correlation ($r_s=-0.83$, $p=0.007$). The highest oocyte abundance was observed during the dry period ($U=0.00007$, $p<0.05$). The minimum abundance of oocytes in May 2009 indicates a reduction in reproductive activity (Fig. 2).

For the entire study period, the mean oocyte diameters for the different stages of gonadal development were $13.90 (\pm 5.45) \mu\text{m}$, $25.17 (\pm 9.20) \mu\text{m}$, $27.46 (\pm 13.52) \mu\text{m}$, $26.32 (\pm 8.64) \mu\text{m}$, and $25.21 (\pm 12.24) \mu\text{m}$ for immature (I), in maturation (II), ripe (III), spawning (IV) and cytolysis (V), respectively. The monthly mean oocyte diameters can be seen in Table 3.

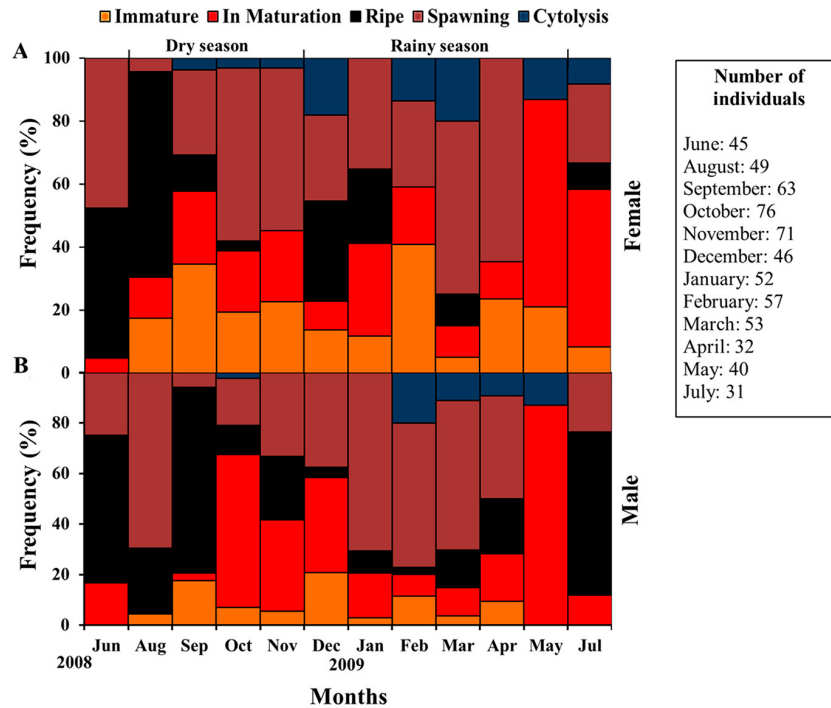


Fig. 6. – Frequency of the different stages of gonadal maturity of (A) males and (B) females between June 2008 and July 2009. Yellow for immature stage; red for in maturation stage; black for ripe stage; brown for spawning stage; blue for cytolysis stage.

Table 2. – Estimated coefficient and standard error (SE) of generalized linear model routines applied to the dependent variables as a function of the independent parameters salinity and rainfall: A, oocyte abundance; B, spawning; C, ripe stage. Values in bold, $p < 0.05$.

	Variables	Coefficient	SE	T	P	AIC
A: Oocyte Abundance	(Intercept)	-1375.05	3607.81	-0.38	0.71	189.10
	Salinity	203.29	90.47	2.25	0.04	
	Rainfall	7.07	7.25	0.98	0.35	
B: Spawning	(Intercept)	4.51	20.60	0.22	0.83	96.42
	Salinity	0.30	0.55	0.54	0.60	
	Rainfall	0.04	0.04	0.82	0.43	
C: Ripe	(Intercept)	0.72	0.41	1.78	0.11	90.86
	Salinity	0.72	0.41	1.78	0.11	
	Rainfall	0.03	0.03	1.01	0.34	

The smallest oocyte size observed was 3.48 μm in May 2009. During this month, a narrow size range of these cells was also noted, varying from 3.48 to 15.67 μm (9.83 ± 3) in stage II and from 5.52 to 14.39 μm (10.28 ± 2.55) in stage III. This month was the period when the gonadal process resumed, as it preceded the period of gametogenic elimination (January 2009 to April 2009).

In the dry season, there was a high frequency of oocytes in the 23 to 28 μm range, where the average diameters of maturation stages II, III, IV and V were located. During the rainy season, there was an increase in the frequency of larger oocytes, within the size class ranges of 33–38 μm and 38–43 μm . The month of May 2009 showed the lowest frequency of oocytes, with the intervals 3 to 8 μm and 8 to 13 μm had the highest frequencies. This month had the highest incidence of immature and maturing individuals, which is why the oocytes were found in the lowest intervals (Fig. 7).

Table 3. – Oocyte diameters of *Leukoma pectorina* (mean $\pm$ standard deviation; min-max). Gonad developmental stages: IM, immature; M, in maturation; RI, ripe; SP, spawning; CT, cytolysis.

Year	Months	Range (min-max)	Mean $\pm$ standard	Sample size	Developmental stage
		(μm)	deviation (μm)		
2008	Jun	9.74–36.07	25.24 $\pm$ 5.62	107	M (II)
		8.76–57.70	27.16 $\pm$ 8.16	1062	RI (III)
		7.67–47.75	26.67 $\pm$ 7.12	1543	SP (IV)
	Aug	7.34–45.97	26.61 $\pm$ 8.18	394	M (II)
		5.37–51.01	27.67 $\pm$ 8.39	2299	RI (III)
		9.67–55.28	27.64 $\pm$ 9.21	141	SP (IV)
		7.91–39.80	20.83 $\pm$ 6.79	518	M (II)
	Sep	6.7–34.79	22.76 $\pm$ 6.47	452	RI (III)
		6.48–40.41	24.08 $\pm$ 7.01	1143	SP (IV)
		9.21–30.33	21.85 $\pm$ 6.92	12	CT (V)
		8–32.98	22.25 $\pm$ 5.51	245	M (II)
	Oct	11.53–31.16	21.07 $\pm$ 4.07	104	RI (III)
		8.38–38.42	22.04 $\pm$ 5.20	1096	SP (IV)
		8.5–42.94	22.61 $\pm$ 6.02	799	M (II)
	Nov	6.33–50.56	21.93 $\pm$ 6.25	2292	SP (IV)
		11.61–48.52	26.95 $\pm$ 6.61	691	RI (III)
		13.05–40.87	26.2 $\pm$ 5.35	452	SP (IV)
		10.18–30.94	17.19 $\pm$ 4.72	47	CT (V)
2009	Jan	3.84–64.76	33.05 $\pm$ 11.50	423	M (II)
		10.87–52.71	31.3 $\pm$ 10.27	668	RI (III)
		8.45–57.37	32.28 $\pm$ 9.63	881	SP (IV)
	Feb	9.11–48.94	25.82 $\pm$ 9.19	298	M (II)
		6.61–46.78	25.60 $\pm$ 9.01	162	SP (IV)
		11.73–48.21	27.26 $\pm$ 9.58	156	CT (V)
		20.67–39.08	31.58 $\pm$ 4.19	99	M (II)
	Mar	13.79–48.43	32.94 $\pm$ 6.58	232	RI (III)
		12.4–56.74	32.45 $\pm$ 6.77	912	SP (IV)
		16.65–44.28	31.7 $\pm$ 6.40	61	CT (V)
		11.06–18.30	14.17 $\pm$ 2.44	10	IM (I)
	Apr	5.35–44	18.36 $\pm$ 10.13	65	M (II)
		5.98–62.14	32.52 $\pm$ 10.51	978	SP (IV)
		3.66–28.74	13.85 $\pm$ 6.67	51	IM (I)
		3.48–15.67	9.83 $\pm$ 3.00	50	M (II)
	May	5.52–14.39	10.28 $\pm$ 2.55	20	CT (V)
		7.21–59.4	26.90 $\pm$ 8.65	879	M (II)
		8.54–39.45	23.05 $\pm$ 5.99	195	RI (III)
		7.54–67.68	26.04 $\pm$ 8.42	471	SP (IV)

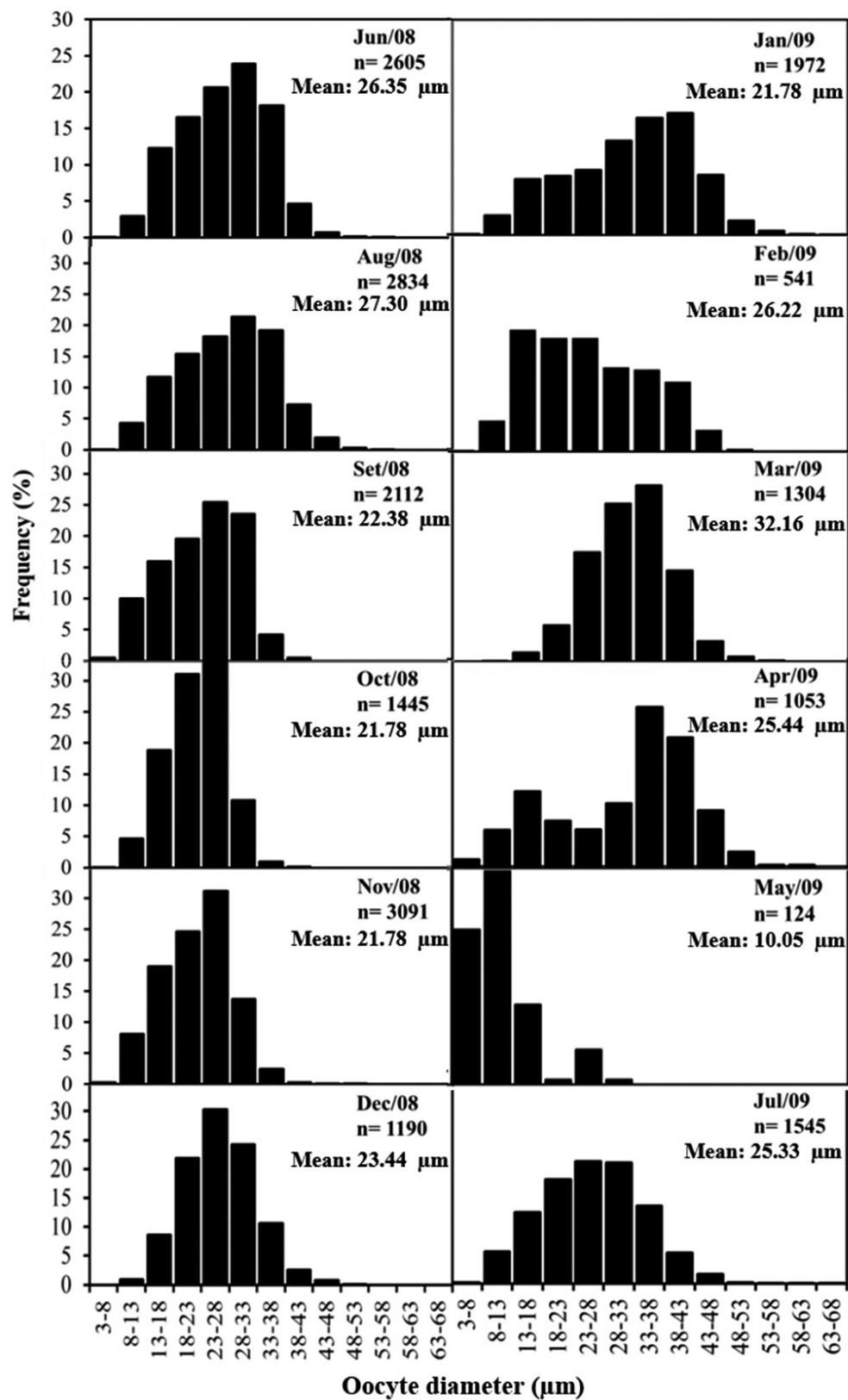


Fig. 7. – Absolute monthly frequency of *L. pectorina* oocyte diameter intervals from June 2008 to July 2009.

DISCUSSION

The population of *L. pectorina* has a predominance of males, which does not follow the pattern described for other similar studied bivalves, such as *Ameghinomya antiqua* (Lozada and Bustos 1984), *Chionopsis crenata* (Borzone et al. 2001), *Callista chione* (Tirado et al. 2002), *Venus verrucosa* (Tirado et al. 2003), *Donax hanleyanus* (Gil and Thomé 2004b), *Tagelus plebeius* (Ceuta and Boehs 2012), *Iphigenia brasiliensis* (Silva et al. 2012) and *Donax striatus* (Gadelha et al. 2019).

Our results show that *L. pectorina* has a long reproductive cycle with continuous spawning, in which males and females mature and eliminate their gametes. This type of strategy is typical of bivalves from tropical environments, corroborating the hypothesis that tropical bivalves have continuous reproduction. Therefore, our results are similar to those of other tropical bivalves that inhabit diverse environments (sandy beach, mangrove, muddy sediments), i.e. *Anomalocardia flexuosa* (Riascos et al. 2007, Lavander et al. 2011, Luz and Boehs 2011), *I. brasiliensis* (Silva et al. 2012), *T. plebeius* (Ceuta and Boehs 2012), *Anadara tuberculosa* (Lucero-Rincón et al. 2013), *L. asperrina* (López et al. 2005) and *Donax striatus* (Gadelha et al. 2019).

Studies of other species of the *Leukoma* genus have reported that they mature at a larger size than *L. pectorina* (11.69 mm). *L. antiqua* reaches its first maturity at 46–48 mm length (Lozada and Bustos 1984) and *L. jodoensis* at 30.1–35 mm length (Kim et al. 2003). However, the results for the size at first maturity of *L. pectorina* are close to those reported for other bivalve species. *Donax hanleyanus* reach sexual maturity at between 12.28 mm and 12.60 mm in Brazil (Gil and Thomé 2004b) and at 13.21 mm in Argentina (Herrmann et al. 2009b); *Iphigenia brasiliensis* reach sexual maturity at 11.4 mm (Silva et al. 2012) and *Donax striatus* at 12.5 mm in Brazil (Gadelha et al. 2019).

Oocyte abundance showed a positive correlation with salinity and a negative correlation with rainfall, and August 2008 (the beginning of the dry season) had the highest oocyte abundance. Therefore, an increase in salinity caused by decreased precipitation during the dry season is a synchronizing factor for the rise in ripe females. This would explain the higher incidence of ripe females in December 2008 and January 2009, which correspond to the end of the dry period, when salinity is still high and precipitation is low. However, *L. pectorina* has very similar mean oocyte diameter values at stages II, III, IV and V, which is related to the type of continuous spawning, since from the ripe stage onwards the follicle has all the female germ cell lineages. Several authors have argued that the almost constant temperature of tropical environments favours a high availability of food all year round, which is the main factor influencing the reproductive cycle of tropical bivalves (Narváez et al. 2000, Freitas et al. 2010, Urban 2000, Gil and Thomé 2004a). According to Gil and Thomé (2004a), water temperature is only an intervening factor in the intensity of reproductive activity.

Studies on other species of *Leukoma* from temperate regions, such as *L. staminea* (Feder et al. 1979), *L. jodoensis* (Kim et al. 2003), and *L. thaca* (Urban and Campos 1994), reveal that they have a seasonal reproductive cycle. In temperate regions, due to climatic conditions, particularly temperature, the seasonal differences are much more pronounced. Suitable conditions for reproduction occur in short periods because environments with low temperatures slow down or halt gonadal maturation and spawning. This contrasts with tropical regions, where climatic conditions, especially the low temperature variation, allow for perennial reproduction. According to Defeo and Cardoso (2002), benthic organisms from low latitudes (tropical and subtropical) have longer reproductive cycles, and these latitudinal trends are related to limited temperature variations and correlate with the high availability of food in the coastal zone.

In tropical countries, rainfall and salinity appear to act as “synchronizing factors”. However, the role of these variables needs to be better understood, as a single environmental variable does not influence reproductive mechanisms in isolation, given the complex interaction between reproductive events and environmental factors (Castillo-Durán et al. 2013, Paixão et al. 2013). López et al. (2005) argue that salinity and rainfall apparently influence gametogenesis, though there is no significant correlation between the variables.

It is important to note that *L. pectorina* undergoes intense exploitation in Marapanim, involving disorderly capture as well as the deterioration of the habitat (including climate change and erosion). Natural and anthropogenic causes may be related to the reduction in the size of first maturation compared with the species of the same genus, which is a reproductive strategy to keep the population in balance (Barbieri et al. 2008, Munroe et al. 2016, Marquardt et al. 2022).

In conclusion, the individuals of *L. pectorina* are gonochoristic, with males predominating and females predominating only at the beginning of the juvenile stage. Both sexes show five stages of gonadal development with distinct follicular and gametogenic characteristics. The presence of all stages of germ cell growth in the ovarian follicle and testicular tubule provides continuous spawning, and the reproductive period includes individuals at different stages of gonadal development, exhibiting a continuous reproductive cycle and reproductive synchronism between males and females. Therefore, *L. pectorina* is a bivalve with r-strategist characteristics.

It is recommended that a tool capable of quickly and efficiently measuring bivalves larger than 15 mm be adopted. This will ensure that only individuals of reproductive size are harvested. Additionally, it is essential to promote environmental education to ensure that these molluscs are harvested, sold and consumed at a size greater than L_{50} . As a suggestion for further studies, we recommend evaluating the effect of sarnambi exploitation on the natural bed.

DECLARATION OF COMPETING INTEREST

The authors of this article declare that they have no financial, professional or personal conflicts of interest that could have inappropriately influenced this work.

ACKNOWLEDGEMENTS

We thank the Universidade Federal Rural da Amazônia for providing the equipment and space necessary for histological analysis.

AUTHORSHIP CONTRIBUTION STATEMENT

Ewertton Souza Gadelha: Conceptualization, Investigation, Formal analysis – original draft, Writing – review & editing. **Ricarla Romilia Viana dos Santos:** Methodology, Formal analysis, Writing – review & editing. **Rosália Furtado Cutrim de Souza:** Formal analysis, Funding acquisition, Methodology, Writing – review & editing.

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