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Research Article

Reproductive cycle of the sand mollusk, *Leukoma pectorina* (Lamarck, 1818)

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ABSTRACT. Knowledge of the reproductive cycle of marine invertebrates is essential to understanding their population dynamics. However, studies on the biological aspects of *Leukoma pectorina* are scarce. This study analyzed the interactions between salinity, temperature, and seston and the reproductive cycle of *L. pectorina* in southern Brazil (27°42'15.6"S, 48°38'23.9"W). In total, 236 specimens were collected between January and December 2022 and subjected to histological analysis to understand their reproductive cycle, sex ratio, onset of maturation, and condition index (CI). *L. pectorina* exhibited a continuous reproductive cycle without any resting phase. The sex ratio between males and females was 1:1.3. Both male and female specimens underwent an initial maturation stage with a minimum shell length of 21 mm. Animals in the spawning stage showed higher CI values than those in the maturation and immature stages. Overall, the reproductive cycle of *L. pectorina* was influenced by temperature and food availability. Temperature stimulated spawning and gametogenesis, and food availability influenced gametogenesis. Salinity did not influence the reproductive cycle of *L. pectorina*.

Keywords: *Leukoma pectorina*; Veneridae; bivalve mollusk; reproductive biology; maturation; gametogenesis

INTRODUCTION

The bivalve *Leukoma pectorina* (Lamarck, 1818) inhabits sandy-silty habitats from the Caribbean to South Brazil (Rios 1994, Lins et al. 2014), having high environmental and socioeconomic importance along its distribution range. Ecotoxicological studies have revealed that *L. pectorina* is a bioindicator of environmental pollutants (Tavares et al. 1988). Moreover, *L. pectorina* is a main food resource and source of income for traditional fishing communities in South America (Borcem et al. 2011, Palheta et al. 2016). However, only a few studies have assessed its population attributes, including the reproductive cycle.

Knowledge about the reproductive cycle is fundamental to understanding gametogenesis, spawning, and mollusk species' larval fixation period. In addition, it reveals these animals' life history, ecology, and behavior (Absher 1989, Arun 2009). Information regarding germ cell differentiation is important in aiding the conservation and recovery of threatened species (Barman et al. 2022).

The reproductive cycle of bivalves is generally annual, consisting of gonad activation, gamete development, maturity, spawning, and rest periods (Da Costa-González et al. 2012). The development of gonadal tissue in bivalves is evaluated via histological techniques, biochemical composition analysis, condition index (CI), and visual observation (Quayle & Newkirk 1989). Among the methods for investigating the reproductive cycle of bivalves are those based on histological analyses (Gosling 2003). Despite being more expensive and time-consuming, these methods provide important and precise information about the development of the gonadal cells (Quayle & Newkirk 1989, Gosling 2003, Da Costa-González et al. 2012).

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The determination of the CI, as well as histological analyses, are widely used to understand reproductive aspects. The CI consists of a relationship between biometric variables that are easy to measure, such as the shell and meat weights (Da Costa-González 2012). Ideally, qualitative methods, such as histological techniques, and quantitative methods, such as the CI test, should be used for species analysis (Gosling 2003, Da Costa-González et al. 2012).

Various environmental factors, such as food availability, salinity, and temperature, affect the reproductive cycle of bivalves (Barreira & Araújo 2005, Da Costa-González et al. 2012, Ke & Li 2013). Changes in the food availability in the environment influence the development of gametes and species spawning (Ke & Li 2003, Darriba et al. 2004, López et al. 2005) and water salinity changes affect animal maturation and spawning (Barreira & Araújo 2005, Suja & Muthiah 2007, Arun 2009).

Temperature is the most studied factor in the literature and exhibits the greatest influence on the reproductive cycle of bivalves (Nichols 1996, Gosling 2003, Darriba et al. 2004, Joaquim et al. 2008, da Costa-González et al. 2012). The increase in temperature influences the beginning of some species' gametogenesis and spawning process (Drummond et al. 2006, Nakamura et al. 2010, Ayache et al. 2016).

Information about the reproductive aspects of *L. pectorina* is an important tool for studies related to larviculture and cultivation of the species. This information would help to reduce over-exploitation, generate income to feed riverside populations, and contribute to increasing diversity of species produced by aquaculture; in Brazil, sand mollusk cultivation is limited to experimental scales (Squella et al. 2015, Santos et al. 2020). In this study, we aimed to evaluate the reproductive aspects of *L. pectorina* via histological analysis and CI.

MATERIALS AND METHODS

Specimens of *L. pectorina* were collected from the municipality of Palhoça city, Barra do Aririu (27°42'15.6"S, 48°38'23.9"W), Brazil (Fig. 1).

Sampling

Specimens of *L. pectorina* (Table 1) were manually collected monthly between January and December 2022 and transported to the Laboratory of Marine Mollusk (LMM, by its Portuguese acronym) of the Federal University of Santa Catarina (UFSC, by its Portuguese acronym). Shell length (mm), width (mm), and height (mm) were measured using calipers, and the total wet weight (g) was measured using a 0.001 g precision scale. Subsequently, the soft tissues of the subsample were removed to determine the CI (n = 91). The histological analysis (n = 145) was performed at the Laboratory of Pathology and Health of Aquatic Organisms (AQUOS, by its Portuguese acronym, UFSC).

Determination of condition index (CI)

From the total number of animals collected, 15 (19-30 mm shell height) were sampled monthly and weighed using a precision scale of 0.001 g. Then, the shells and soft parts of the animals were separated. The shells were kept at room temperature for 24 h and then weighed to obtain the shell weight, while the soft parts of the animals were weighed as soon as they were removed from the shells to get the wet weight. After weighing, the soft parts were dried in an oven at 68°C for 48 h. At the end of this procedure, the soft parts were weighed again to obtain the dry weight. The formula reported by Crosby & Gale (1990) was used to determine the CI:

$$CI = (\text{soft dry tissue weight} / \text{total weight - shell weight}) \times 100$$

Environmental variables

Seawater salinity and temperature (ºC) were determined monthly *in situ* using the NQRF-32ATC portable refractometer and a manual thermometer.

For seston analysis, water samples (0.30 m deep) were collected monthly at the collection point and stored in dark glass bottles (500 mL) in the cold for subsequent analysis. Total particulate matter (TPM), particulate organic matter (POM), and particulate inorganic matter (PIM) concentrations were determined using the gravimetric filtration method as described by Strickland & Parsons (1972), with some modifications. Briefly, the water sample (250 mL) was double-filtered through the Whatman GF/C glass fiber microfilters (0.48 μm porosity and 47 mm diameter), washed with distilled water, calcinated, and weighed. After filtration, 5 mL of ammonium formate was added to remove salt from the sample. The filters were then placed in an oven for 48 h and weighed to determine the TPM concentration. Next, they were burned in a muffle furnace (460°C) for four hours and subsequently weighed to determine the POM and PIM concentrations.

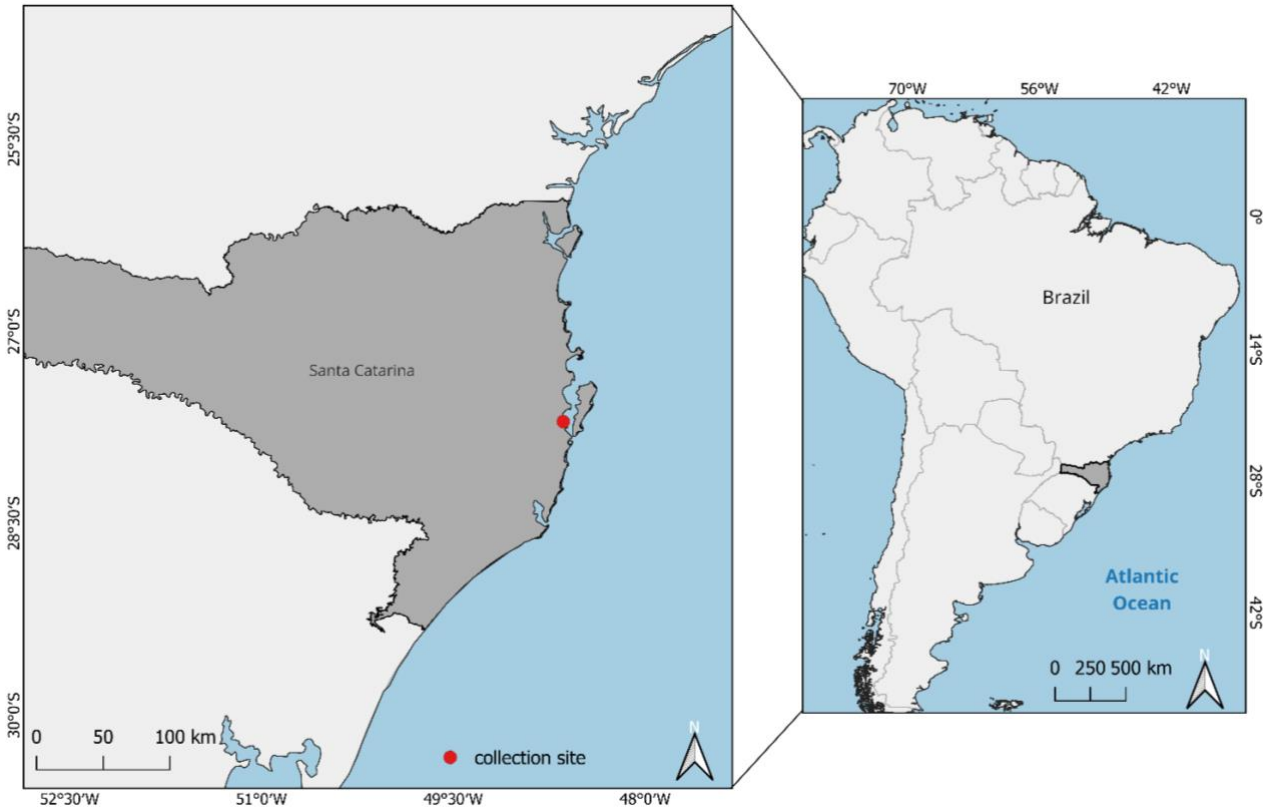

Figure 1. Location of the study area in the municipality of Palhoça city, Santa Catarina, Brazil.

Table 1. The total number of animals sampled during the study, the number of animals used to determine the condition index (CI), and histological analyses. [a]Used to measure shell dimensions and wet weight (Fig. 7), [b]used to determine CI (Fig. 6), and [c]used in histological analyses (Fig. 4). November is not included in the table due to the absence of *Leukoma pectorina* at the collection site this month.

Months	Total Nº sampled animals[a]	Nº of animals used in CI analysis[b]	Nº of animals used in histological analysis[c]
January	37	16	20
February	22	3	15
March	47	11	12
April	120	14	15
May	26	12	14
June	5	-	5
July	22	9	13
August	73	8	15
September	10	-	10
October	18	7	11
December	26	11	15
Total	**406**	**91**	**145**

Histological analyses

Soft tissues of 145 organisms were removed for histological analysis, kept in a marine Davison fixative solution for 48 h, and preserved in 70% alcohol until processing. After fixation, a transverse section from a portion of gonad tissue located at the dorsal portion of the foot was obtained to prepare 4-mm thick sections. Tissues were placed in cassettes for various procedures, such as progressive baths of alcohol, xylene, and paraffin, and then embedded in paraffin blocks. Sections of 7 µm thickness were cut using a microtome, placed on glass slides, and stained with eosin and hematoxylin.

Histological slides were analyzed via optical microscopy to determine the reproductive cycle phase and sex. Phases of the reproductive cycle were determined with adaptations as described by Xie & Burnell (1994).

Statistical analyses

CI, shell height (mm), shell width (mm), shell length (mm), and weight (g) in the sampled individuals of *L. pectorina* were analyzed using analysis of variance, and the means were compared using the Tukey-Kramer test. A *t*-test was performed via permutation to analyze the gonadal tissue development. All data were analyzed using the SAS statistical program. The significance level was set at 5%.

RESULTS

Developmental phases using the histological analysis of the gonadal tissues in females and males of *L. pectorina* were determined based on the criteria described by Xie & Burnell (1994) (Figs. 2-3).

Female

In the pre-maturation phase (Fig. 2a), an increase in the number of oocytes in the acinus walls is observed; small oocytes and few free oocytes were observed in the lumen. In the maturation phase (Fig. 2b), a decrease in connective tissue and free oocytes in the lumen was observed, but in smaller quantities than the total number of oocytes in the acinus. Oocytes of various sizes were also observed in abundance. In the mature phase (Fig. 2c), the gonads filled a large part of the surface, the majority of oocytes were free in the lumen with a polygonal configuration, and the acinus wall was thin. In the partial spawning phase (Fig. 2d), a reduced number of free oocytes was observed in the acinus after the release of gametes. In the spawning and absorption phase (Fig. 2e), there were ruptured and relatively empty acini. Only oogonia and residual oocytes were found in the acini, most undergoing reabsorption. The presence of phagocytes was observed.

Male

In the pre-maturation phase (Fig. 3a), the beginning of gonadal proliferation and the presence of spermatogonia, spermatocytes, and spermatids in the acini were observed. No sperm was observed. In the maturation phase (Fig. 3b), spermatogonia, spermatocytes, spermatids, and spermatozoa coexisted in the acini. The majority of acini were filled with spermatozoa. In the mature phase (Fig. 3c), juxtaposed acini densely filled with spermatozoa were observed, with their tail pointing toward the center of the lumen. In the partial spawning phase (Fig. 3d), spermatozoa were responsible for most follicle cells. Empty spaces were observed in some acini due to the release of sperm. Finally, in the spawning and absorption phase (Fig. 3e), the acini were ruptured and relatively empty, with only residual spermatozoa found and reabsorbed in the acini.

Gonadal cycle

Histological analyses revealed no differences among individuals of *L. pectorina* found in the pre-maturation, maturation, mature, and spawning phases throughout the year (Fig. 4). Interestingly, this species did not exhibit a resting phase, and only the pre-maturation, maturation, and spawning phases were observed throughout the study. Of the 145 individuals evaluated in this study, 63 were males, and 82 were females, with a male-to-female ratio of 1:1.30. No hermaphrodites were observed.

Gametogenesis was observed in the sampled organisms throughout the year. No individuals in the pre-maturation phase were observed in January, February, June, and July. No individuals in the maturation phase were observed in February, May, and July. High percentages of individuals in the pre-maturation (25 and 13%) and maturation (17 and 33%) stages were observed in March and April, respectively, and low percentages were observed in August (0.07%). Mature individuals were observed throughout the year, except in May and October. The highest percentage of mature animals was observed in June (40%), and the lowest in April (0.07%).

This species spawned throughout the year. The highest percentage of individuals in the partial spawning phase was observed in July (62%), while the lowest percentage was observed in February (13%) and April (13%). The highest and lowest percentages of individuals in the spawning and absorption phases were observed in May (64%) and September (10%), respectively.

In the initial maturation phase, both males and females exhibited a minimum shell length of 21 mm. In contrast, mature individuals exhibited minimum shell lengths of 21 mm for females and 25 mm for males (Fig. 5).

Condition index (CI)

CI values varied significantly in the individuals sampled in January, March, April, and May compared to those sampled in October and December. Only the CI values for February, July, and August did not show

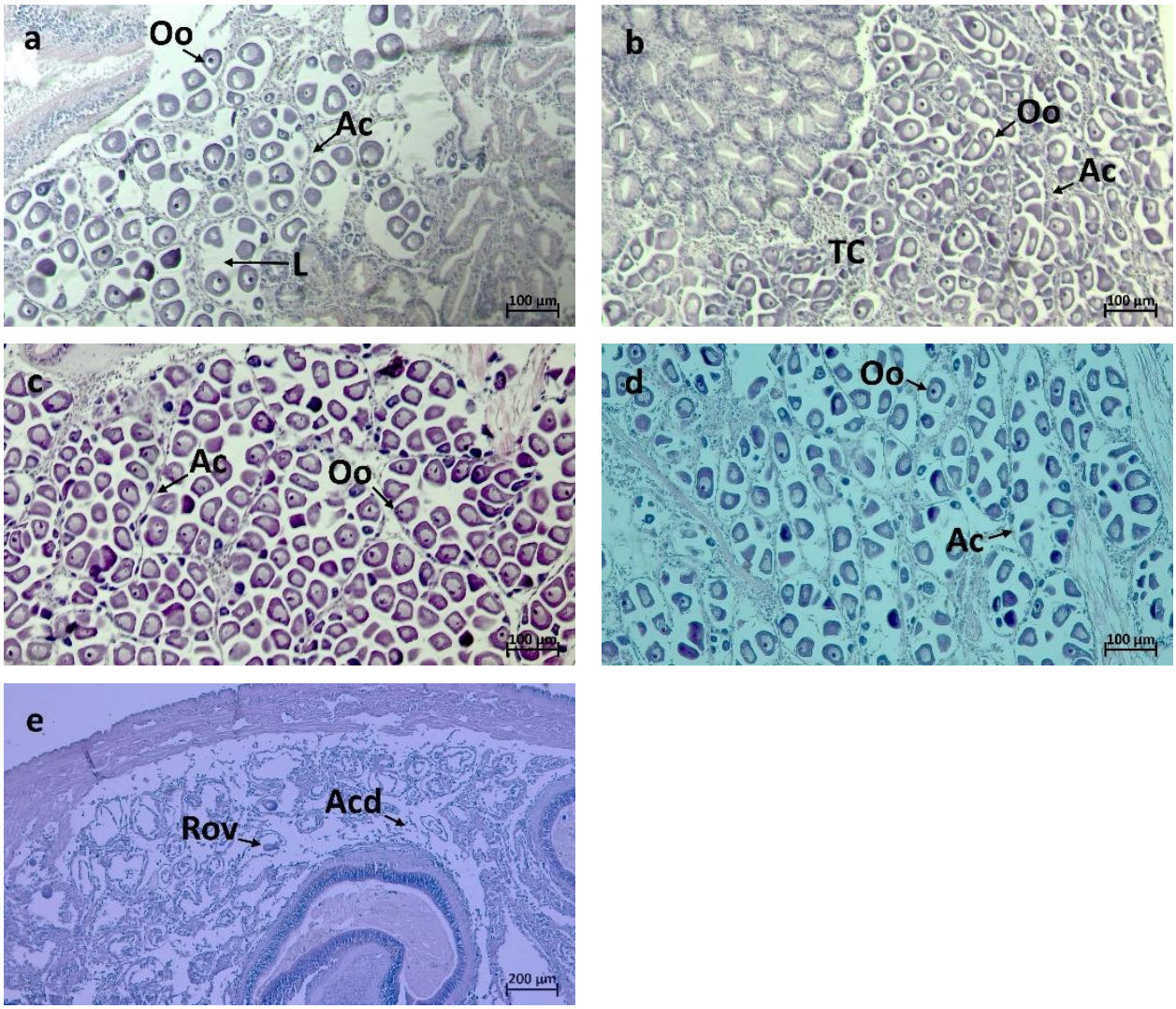

Figure 2. Stages of gonadic tissue development in females of *Leukoma pectorina*. a) Pre-maturation, b) maturation, c) mature, d) partial spawning, and e) spawning and absorption phases. Oo: oocyte, Ac: acinus, L: lumen, Tc: connective tissue, Rov: oocyte waste, Acd: acinus wall degradation.

significant differences with the CI values observed in the other months of the year (Fig. 6).

CI value was the highest in the individuals sampled in October (140.95 ± 16.60), followed by those sampled in February (138.37 ± 30.45) and those sampled in December (133.51 ± 42.17). Histological analyses revealed that 55, 13, and 40% of the individuals were in the partial spawning phase, and 18, 53, and 20% were in the spawning and absorption phase in individuals sampled in October, February, and December, respectively.

In October, individuals in the pre-maturation and maturation stages constituted 18 and 9% of the analyzed samples. In December, individuals in the pre-maturation and maturation stages only constituted 13% of the analyzed samples. No individuals were observed in these two gonadal phases in February. Mature individuals were observed in February and December, accounting for 33 and 13% of the analyzed samples, respectively; no individuals in this phase were observed in October.

Individuals collected in January had the lowest CI value (83.02 ± 19.82), followed by those collected in March (83.49 ± 36.14) and April (87.92 ± 20.10). In January, 15% of the individuals were in the maturation phase, 35% were mature, 20% were in partial spawning, and 30% were in spawning and absorption phase. No premature infants were observed in January.

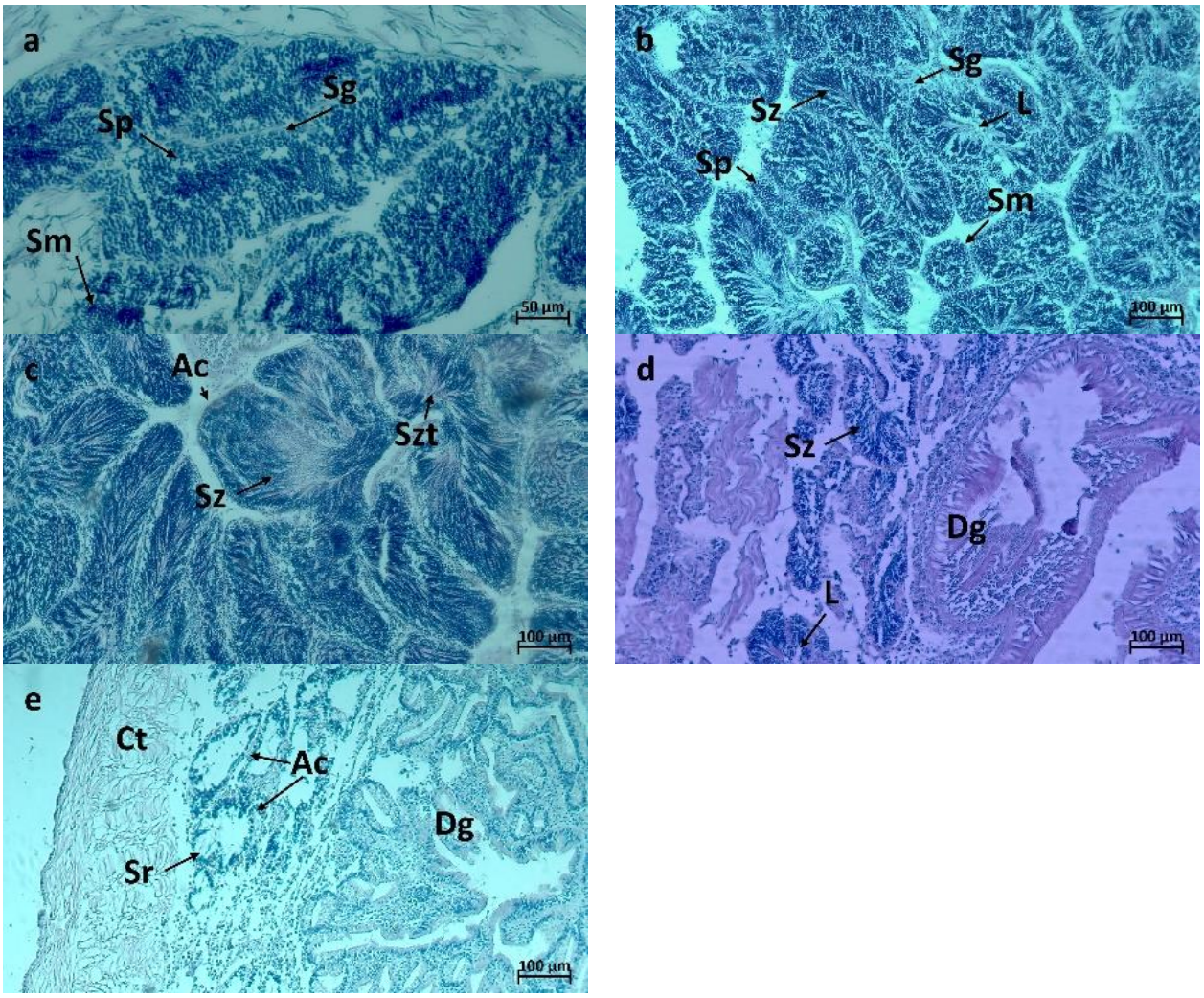

Figure 3. Stages of gonadic tissue development in males of *Leukoma pectorina*. a) Pre-maturation, b) maturation, c) mature, d) partial spawning, and e) spawning and absorption phases. Sg: spermatogonia, Sp: spermatocyte, Sm: spermatid, Sz: sperm, SzT: sperm tail, Sr: sperm residue, Ac: acinus, L: lumen, Ct: connective tissue, Dg: digestive glands.

In March and April, pre-maturation individuals accounted for 25 and 13%, maturing individuals for 17 and 33%, mature individuals for 8 and 7%, partially spawned animals for 17 and 13%, and spawning and absorption individuals for 33% (both months) of the analyzed samples in the two months, respectively.

Biometric analyses

Values of the average shell height of the individuals ranged from 26 ± 2.58 to 15.45 ± 0.52 mm in January and December. In May and December, the values of the average shell length ranged from 29.67 ± 2.50 to 18.73 ± 0.79 mm, respectively. The values of the average shell width in January and December ranged from 17.38 ± 1.45 to 10.36 ± 0.50 mm (Fig. 7), respectively. Values of the average weight ranged from 9.44 ± 2.24 and 1.95 ± 0.23 g in January and December.

A significant difference in the values of the shell height was observed in all months compared with that in December ($P < 0.05$). Values of shell height in January were significantly different compared to those from October (Fig. 7a). A significant difference in the values of shell length was observed in all months compared to those observed in December. Values of the shell lengths of the species in January and May also showed a significant difference compared to those in March, July, and October (Fig. 7b).

A significant difference ($P < 0.05$) in the values of the shell width of *L. pectorina* was observed in all months compared to that observed in December. In

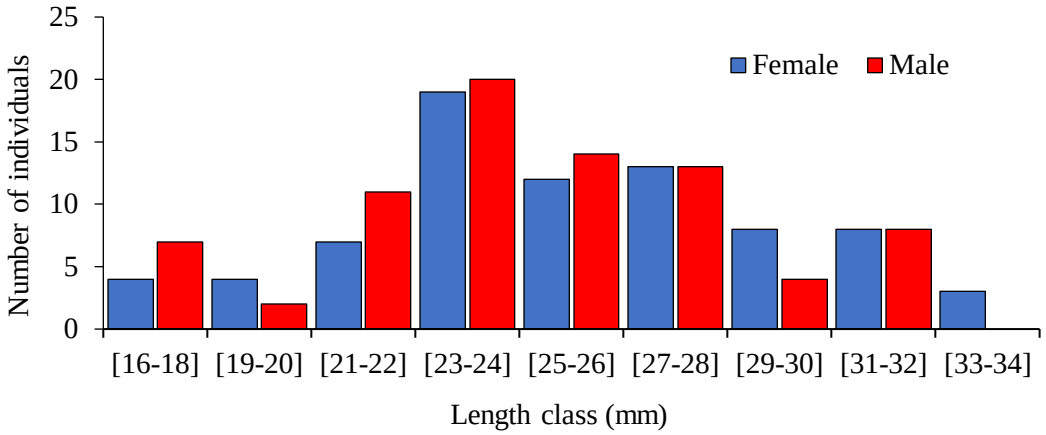

Figure 4. Proportions of individuals of *Leukoma pectorina* at different maturation stages (according to the gonadic tissue development) recorded during the different sampled months. In November, no individuals were observed at the sampling site.

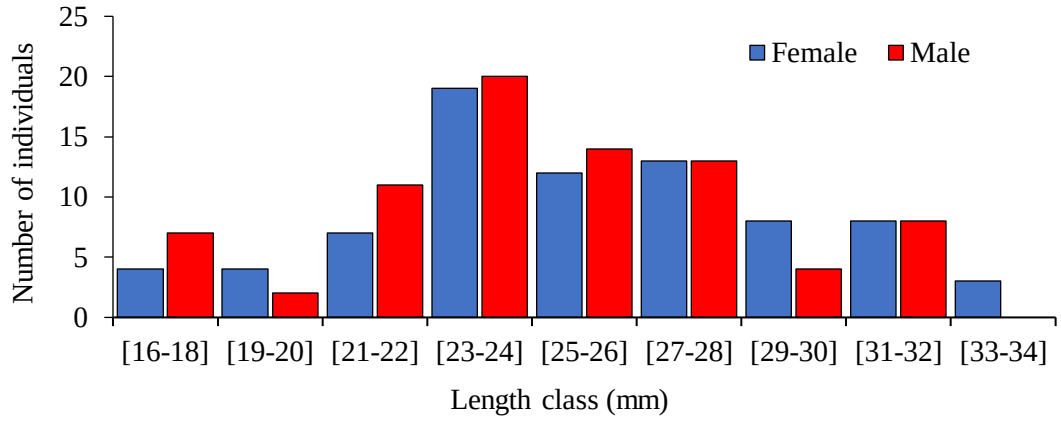

Figure 5. Shell length (mm) size distribution of the total number of individuals of *Leukoma pectorina* analyzed in the present study by sex.

January, April, and May, values of the width of the species also showed a significant difference ($P < 0.05$) compared to those observed in March and July (Fig. 7c). Weight of *L. pectorina* showed a significant difference ($P < 0.05$) in all months compared to that in December. In January, March, and April, weight significantly differed from that observed in July (Fig. 7d).

Environmental variables

Temperature

The water temperature was highest in January (29°C) and lowest in June (17°C). In July, it increased to 18°C and continued to increase until it reached 25°C in December (Fig. 8).

Salinity

Salinity varied between 29 and 34 from January to July (Fig. 8). In August, the salinity decreased to 28 and remained constant until October, when it reached 25. It increased to 29 in November and dropped sharply to 22 in December, the lowest value recorded throughout the year. The highest salinity (34) was recorded in March and July.

Seston

TPM and PIM varied considerably throughout the year (Fig. 9), with the lowest levels in January (13.22 and 10.88 mg L^{-1}, respectively) and the highest in April (96.74 and 71.30 mg L^{-1}, respectively). POM level was the lowest in January (2.34 mg L^{-1}) and highest in March (47.38 mg L^{-1}); it decreased to 25.44 mg L^{-1} in April and fell further to 17.60 mg L^{-1} in May. Little varia-

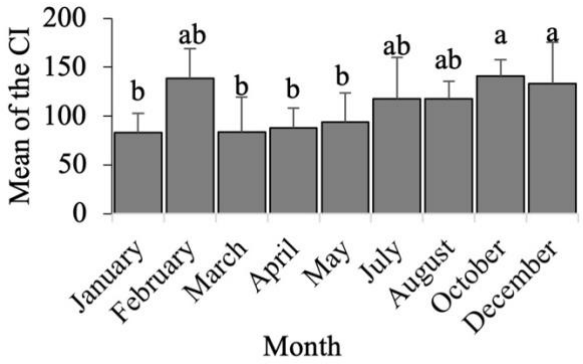

Figure 6. Mean and standard deviation of the condition index (CI) of *Leukoma pectorina* across different months. Different letters indicate the significant differences in the CI values of different months determined using the Tukey-Kramer test. The graph does not include September to November due to the absence of this species at the collection site during these months.

tion in POM levels was observed in the remainder of the year (17.60-25.84 mg L^{-1}).

DISCUSSION

The reproductive cycle of bivalves is affected by its geographic location and the interactions between exogenous (i.e. salinity, temperature, and food availability), and endogenous (i.e. food reserves, genotype, and endocrine factors). The relationship between these factors is also responsible for the reproductive patterns recorded in the bivalve mollusks (Maia et al. 2006, Da Costa-González 2012). Bivalves inhabiting tropical regions exhibit a continuous reproductive pattern, adopting reproductive strategies such as the intense proliferation of mature gametes and synchronous and asynchronous spawning during specific periods (Cárdenas & Aranda 2000). Food availability throughout the year and low variations in temperature are favorable for the reproduction of species as there is no food competition, and temperature variations in the tropics do not affect the metabolism of animals as intensely as they do in temperate regions (Cárdenas & Aranda 2000, Gadelha & Melo 2017).

The sex ratio pattern observed in *L. pectorina* in the present study is under the patterns found in studies carried out with *Marcia opima* (Suja & Muthiah 2007), *Villorita cyprinoides* (Arun 2009), *Megapitaria aurantiaca* (García-Domínguez et al. 1994), and *Anomalocardia flexuosa* (Lavander et al. 2011) which also had a higher proportion of females than males. In the present study, the predominance of females may indicate a strategy adopted by *L. pectorina*, owing to the habitat in which it was found, to achieve successful reproduction. Sex ratio with a prevalence of females is a strategy adopted by some bivalve mollusks to maximize the reproductive success of the species (Gadelha & Melo 2017, Barman et al. 2022). According to Mzighani (2005), the fact that bivalves present protandric sexual reversion would explain the female prevalence in some environments. Morton (1991) suggested that the predominance of female animals is a strategy for reproductive success in regions with great environmental variation, as the energy demand must be greater for oogenesis to be successful.

The results of the present study align with those of studies conducted on the sand mollusks *Mesodesma mactroides* (=*Amarilladesma mactroides*) (Herrmann et al. 2009) and *Venerupis corrugata* (Joaquim et al. 2011), which showed a negative relationship between the values of CI and histological analyses. CI value provides quick information about the reproductive conditions of animals and is generally associated with the maturation and spawning of bivalves. High values are typically associated with the maturation phase, whereas low values are associated with the spawning phase (Christo et al. 2016, Vidya et al. 2020, Barman et al. 2022). It is important to highlight that the CI values obtained in this study do not agree with the results commonly found in the literature regarding the relationship between CI and the gametogenic cycle of bivalves, which tend to present the highest CI value in mature individuals. In the present study, the highest CI values were observed in individuals in the spawning phase. A possible explanation for this finding is the continuous reproductive pattern adopted by the species, which is responsible for rapid recovery, followed by the accumulation of reserves to be used in the subsequent process of gametogenesis.

Knowledge of the size at which the first maturation of bivalves occurs is important to understand the population characteristics of each species, as the initiation of sexual maturation is a reproductive strategy that varies according to region and is influenced by exogenous and environmental factors and anthropogenic pressure (Bayne 1973, Cárdenas & Aranda 2000, Gadelha & Melo 2017). According to our results, the initial maturation of the individuals is reached at about 21 mm in shell length. However, this value should be taken cautiously, considering that few individuals smaller than 20 mm were found in the present study. This approximate value can be corroborated with future studies in which a larger number of individuals from the smaller size range can

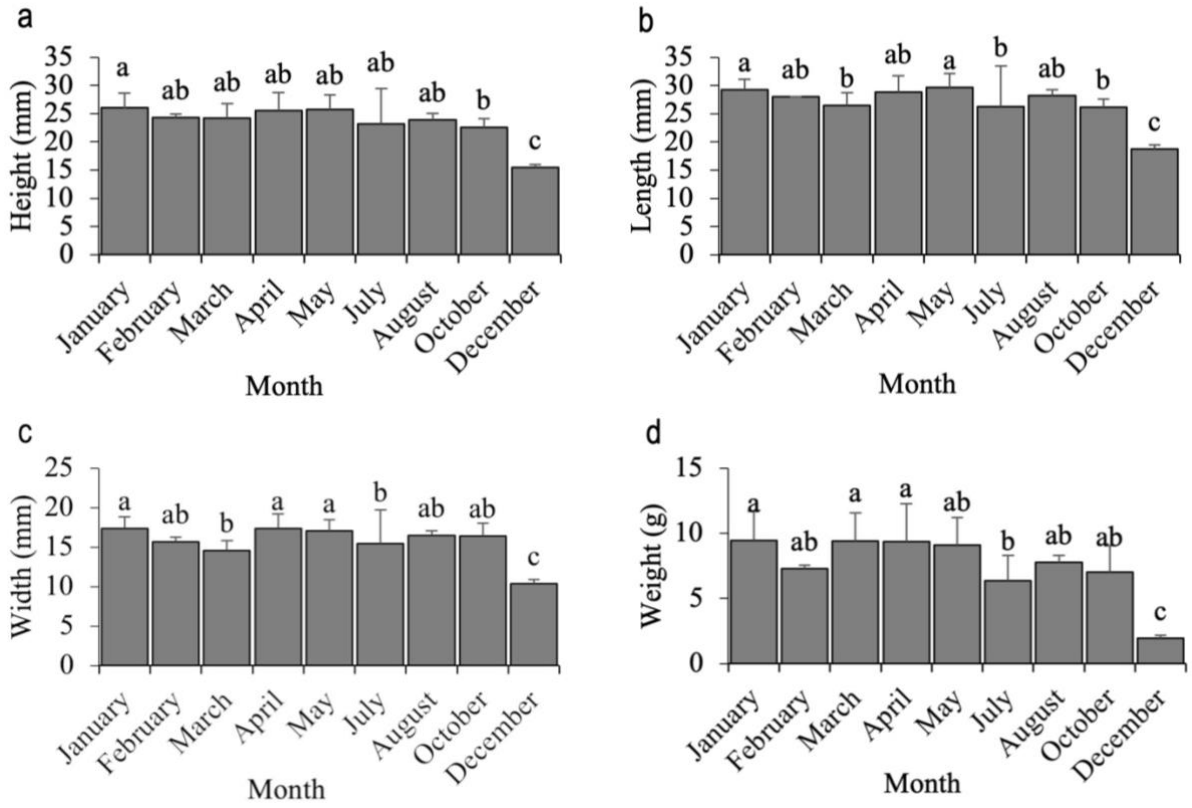

Figure 7. Mean and standard deviation of the a) shell height (mm), b) shell length (mm), c) shell width (mm), and d) total weight (g) of *Leukoma pectorina* across different months. Different letters indicate the significant differences in the height, length, width, and weight of this species in different months, as determined using the Tukey-Kramer test. The graph does not include June, September, and November due to the absence of this species at the collection site during these months.

be obtained. However, the results were similar to those reported in studies on *Anomalocardia flexuosa* (Barreira & Araújo 2005), *Donax hanleyanus* (Gil & Thomé 2004b), and *Iphigenia brasiliensis* (Silva et al. 2012) in Brazil, a region with a tropical climate. Bivalves that inhabit low-latitude regions adopt an opportunistic reproductive strategy, which consists of directing the energy acquired through food towards the maturation of gonads instead of storing it in the somatic tissue (Bayne 1973, Cárdenas & Aranda 2000, Da Costa-González 2012). Food is abundant throughout the year in tropical regions. Thus, species usually adopt a continuous reproductive cycle pattern, as they have sufficient energy to mature gametes. As a result, tropical species are usually present at the beginning of maturation in smaller sizes than bivalves from temperate regions (Cárdenas & Aranda 2000, Da Costa-González et al. 2012).

Temperature is an important environmental factor affecting bivalves' reproductive cycle, mainly the maturation and spawning (Gosling 2003, Arun 2009, Da Costa-González 2012). In a study on *Leukoma asperrima*, López et al. (2005) observed that a drop in temperature increased the percentage of animals in the spawning and gametogenesis phases. However, in a study on *Puberella crenata*, Borzone et al. (2001) found that the species presented spawning periods with increasing temperatures, and gametogenesis peaked in autumn and spring. Similarly, an increase in temperature was also responsible for the spawning of *Anomalocardia flexuosa* (Corte 2015), and gametogenesis peaks occurred at the end of summer and the beginning of spring. The results of the present study corroborate those mentioned above since the species has a continuous reproductive cycle and present peaks in spawning and gametogenesis, both during increasing and decreasing temperatures. Temperature variations stimulated gametogenesis and spawning of *L. pectorina*, acting mainly on the intensity of the species' reproductive phases, as the maturation and elimination of gametes were predominant throughout the months analyzed.

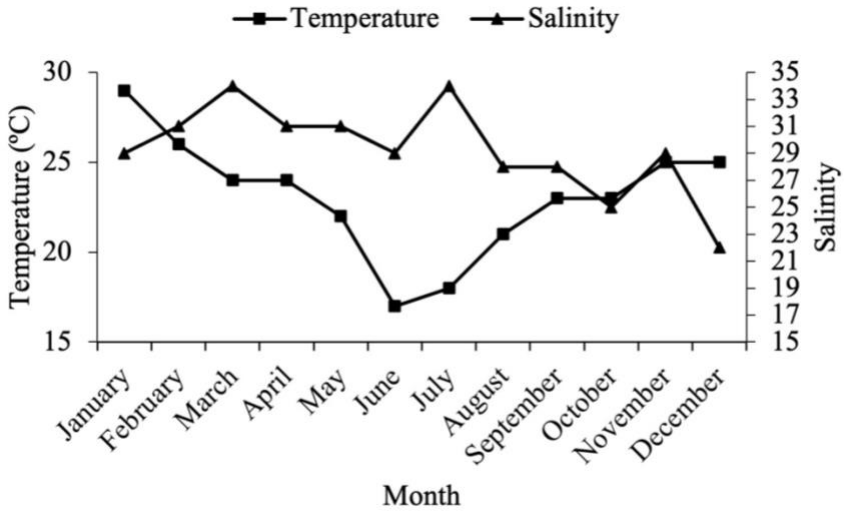

Figure 8. Water temperature (ºC) and salinity in Palhoça (Santa Catarina, Brazil) in different months.

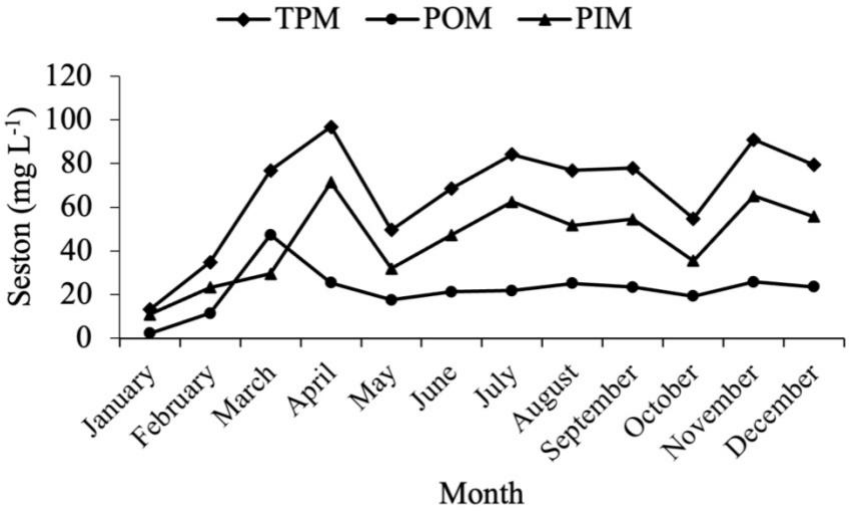

Figure 9. Total particulate matter (TPM), particulate organic matter (POM), and particulate inorganic matter (PIM) in Palhoça (Santa Catarina, Brazil) in different months.

Salinity is an environmental variable affecting gonadal maturation, spawning, gamete release, and sex determination in bivalves (Barreira & Araújo 2005, Suja & Muthiah 2007, Lenz & Boehs 2011, Paixão et al. 2013). Arun (2009) reported that a decrease in salinity influences the spawning of *Villorita cyprinoides*. In contrast, an increase in salinity triggers the spawning phase in *Marcia opima* (Suja & Muthiah 2007). Vázquez et al. (2021) reported that low salinity delays the initiation of gametogenesis in *Ruditapes decussatus*, *Ruditapes philippinarum*, *Venerupis corrugata*, and *Cerastoderma edule*. Here, no relationship was observed between salinity variation and the reproductive cycle of *L. pectorina*. Similarly, the reproductive cycle is influenced by temperature, but not variable salinity, in the sand mollusk *Donax hanleyanus* (Gil & Thomé 2004a). According to the present results, temperature influenced the intensity of the reproductive phases. However, salinity did not influence the reproductive cycle of *L. pectorina*. Our findings are in agreement with those of studies conducted in tropical regions with the sand mollusks *Anomalocardia flexuosa* (Narchi 1976), *L. asperrima* (López et al. 2005), and *Tivela mactroides* (Denadai et al. 2015), indicating that the reproductive pattern adopted by the mollusk is a function of interactions with the environment where the organisms are living.

Food availability is directly linked to the spawning of bivalve mollusks, which influences population abundance, recruitment, and growth or survival of the

species (Darriba et al. 2004, López et al. 2005, Corte et al. 2017). An abundance of food in the environment (phytoplankton and particulate matter) affects the gametogenic development and sexual maturation of bivalves, as these reproductive phases of mollusks are closely linked to the accumulation of nutrients (Da Costa-González et al. 2012).

In Spain, Darriba et al. (2004) reported that gametogenesis and spawning are initiated with the decrease in phytoplankton levels in *Ensis magnus*. In China, Yan et al. (2010) reported that *Cyclina sinensis* spawns during the phytoplankton bloom period, and the gametogenesis phase begins when food in the environment decreases. In Chile, Stead et al. (1997) revealed that gametogenic development and spawning in *Ameghinomya antiqua* occur when phytoplankton and seston are abundant in the environment. The same pattern was observed by López et al. (2005) in *Leukoma asperrima* in Panama. Our results are consistent with those reported by Stead et al. (1997) and López et al. (2005) on species maturation, as a positive relationship was observed between the abundance of food and gametogenesis in *L. pectorina* in this study. The species' reproductive behavior indicated that spawning was not influenced by the change in food availability in the environment. In the tropics, competition for food is scarce as food availability shows little variation throughout the year (Gadelha & Melo 2017). Therefore, nutrients obtained from food are used for the gametogenic development of the species, and partial spawning occurs throughout the year as ample food is available for the development of larvae after release into the environment (Gil & Thomé 2004a, López et al. 2005, Ke & Li 2013).

CONCLUSIONS

In this study, *L. pectorina* exhibited a continuous reproductive cycle, predominating females over males and an initial maturation length of 21 mm in both males and females. CI was found to be an inadequate indicator of species maturation, as the highest CI values were observed in animals in the spawning phase. Environmental factor analysis revealed that temperature influenced the intensity of the reproductive phases. Notably, maturation and spawning occurred throughout the study period. However, salinity did not influence the reproductive cycle of *L. pectorina.* Moreover, food availability in the environment only influenced the maturation phase, not the spawning phase, in *L. pectorina*.

Credit author contribution

A.C. da Silva: methodology, formal analysis, writing-original draft; C.H.A. de Miranda Gomes: methodology, validation, review, and editing; T.B. Freire: methodology, review, and editing; C.M.R de Melo: funding acquisition, project administration, supervision, methodology, formal analysis, review, and editing.

Declaration of competing interest

The authors declare no conflicts of interest.

Research data

Supplementary data to this article can be found online at https://doi.org/10.17632/dphdhndgwx.1

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