NOTE

Reproductive cycle of *Tagelus adansonii* in the Joal-Fadiouth lagoon, Senegal

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ABSTRACT. Very little is known about the reproductive biology of burrowing bivalve species found along the Senegalese coast, despite their cultural and economic importance for the local population. Knowledge of the reproductive cycle of these bivalve mollusks is very important not only for the management of this resource in the natural environment, but also for the development of bivalve mollusk farming. *Tagelus adansonii* is a bivalve mollusk widely distributed in the mangrove ecosystems of the West African coast. In this study, 360 individuals were sampled from the Joal-Fadiouth lagoon in Senegal over a twelve-month period. Histological sections from these samples showed that *T. adansonii* is a gonochoric species, with only one case of hermaphroditism detected. The reproduction of *T. adansonii* in the lagoon was continuous. The maturation and spawning stages were maximal (80%) in July and August, while the early gametogenesis stage was maximal in May. The high gamete emission seems to be favored by lower salinity and higher temperature.

Key words: Bivalve biology, gametogenesis.

Ciclo reproductivo de *Tagelus adansonii* en la laguna de Joal-Fadiouth, Senegal

RESUMEN. A pesar de su importancia cultural y económica para la población local, se sabe muy poco sobre la biología reproductiva de las especies de bivalvos excavadores que se encuentran a lo largo de la costa senegalesa. El conocimiento del ciclo reproductivo de estos moluscos bivalvos es muy importante no solo para la gestión de este recurso en el entorno natural, sino también para el desarrollo del cultivo de moluscos bivalvos. *Tagelus adansonii* es un molusco bivalvo ampliamente distribuido en los ecosistemas de manglares de la costa occidental africana. En este estudio, se muestrearon 360 individuos de la laguna de Joal-Fadiouth en Senegal durante un período de doce meses. Las secciones histológicas de estas muestras indicaron que *T. adansonii* es una especie gonocórica, con solo un caso de hermafroditismo detectado. La reproducción de *T. adansonii* en la laguna fue continua. Las etapas de maduración y desove fueron máximas (80%) en julio y agosto, mientras que la etapa de gametogénesis temprana fue máxima en mayo. La alta emisión de gametos parece ser favorecida por una menor salinidad y una temperatura más alta.

Palabras clave: Biología de bivalvos, gametogénesis.

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According to Cosel and Gofas (2019), the West African coast exhibits a high diversity of bivalve species, accounting for 308 species. Despite this great diversity, only a few of these species have been identified and studied. In fact, studies on the reproduction of bivalves on the Senegalese coast have mainly focused on two species: *Senilia senilis* and *Crassostrea tulipa* (Seck 1986; Diadhiou 1995; Diouf 2014; Sané et al 2023; Thiao et al 2024). *Tagelus adansonii* (Bosc, 1801), an endobenthic bivalve species, is popular in Guinea Bissau (Diouf et al. 2017) and Nigeria (Udo et al. 2022), although it is not exploited in Senegal (Diouf 2024). In many other countries, this genus includes species that are valuable for artisanal fishers not only as a food source, but also economically to make their livings (Silva et al. 2014). This study is of particular importance in the current context, which is characterized by a notorious decline in bivalve mollusk stocks (De Morais et al. 2007; Desrosiers 2013). The aim of this study was to describe the different reproductive stages of *T. adansonii* and analyze their relationship with seasonal variations in climate and ocean currents.

This study was carried out in the Joal-Fadiouth lagoon, on the west of the Senegalese maritime border. It occupies the southern tip of the Thiès region, between 14° 06′ N and 13° 13′ N and 16° 47′ W and 16° 53′ W, on the small coast. Individuals were collected at the Toumoulane station, which is located near the main bridge connecting the island of Fadiouth with Joal (Figure 1). Monthly samplings were conducted for 12 months, from May 2019 to May 2020 (except for March 2020, when Covid-19 travel restrictions prevented sampling). Approximately 30 individuals > 40 mm were collected monthly, for a total of 360 individuals. Samples were measured and then immersed in Davidson's fixative for 48 h and then preserved in 70% ethanol solution. After that, they were dehydrated, paraffin-embedded, sectioned and placed on a microscope slide before being rehydrated, stained with aqueous dyes (hematoxylin and eosin), rinsed and dehydrated again. Finally, they were covered with a slide after a few drops of resin had been applied. The *Chi*^{2} test was used to test if the sex ratio of the studied populations showed a sex ratio different from 1:1.

The gonad of *T. adansonii* was located in the visceral mass, covered by a simple epithelium. The

• Sampling site

Figure 1. Sample collection site for histological study of *Tagelus adansonii*, at Joal-Fadiouth lagoon, western Senegal.

space occupied by the gonad varied depending on the stage of maturation of sex cells. When sex cells were undeveloped, the gonad occupied a restricted area located in the medio-lateral and postero-anterior parts of the visceral mass (Figure 2 A-C). In contrast, when sex cells were developed, the gonad surrounded the digestive gland and even extended into the foot muscle (Figure 2 D). The gonad was composed of follicle cells (nourishing connective tissue) and germ cells (sex cells). Germ cells were arranged in gonadal tubules where they carry out gametogenesis. These gonadal tubules were in turn surrounded by connective tissue, which tends to shrink as the tubules enlarge. Gonadal tubules were at the same stage of development, indicating that maturation was synchronous. However, within the same gonadal tubule, sex cells were at different stages of development. There was no sexual dimorphism in *T. adansonii*. Only one case of hermaphroditism was observed during this sampling, while the rest of the observations showed separate sexes (gonochoric).

For this study, the work of Cledón et al. (2004) and Farias (2008) have been used as a reference to distinguish different stages of reproduction for *T. adansonii*. Five female stages and four male stages were characterized for *T. adansonii*. Stages were defined according to the development of the sex cells, their number in the tubules and the size of the interfollicular space. In the undifferentiated stage, the gonadal surface occupied a limited space. Individuals showed a small number of gonadal tubules containing undifferentiated germ cells (ovogonia or spermatogonia) in the area where gonads were located (Figure 3).

Female reproductive stages were:

- Early gametogenesis: at the onset of gametogenesis, the size and number of gonadal tubules increased slightly. Small or growing oocytes with dark cytoplasm and large nuclei were clearly visible in almost all gonadal tubules. The nucleolus was visible in some germ cells. The lumen of the gonadal tubules was very wide and empty

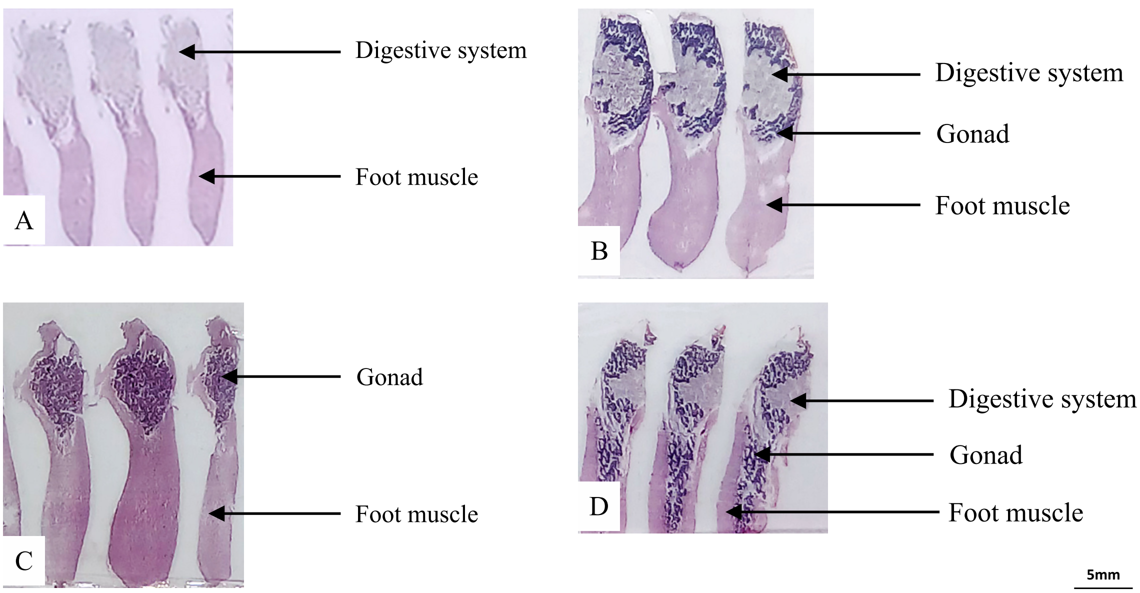

Figure 2. Location of gonads in the visceral mass and foot of *Tagelus adansonii* on histological sections. A) Sagittal section showing a poorly developed gonad. B) Superficial longitudinal section showing the developed gonad laterally surrounding the digestive tract. C) Sagittal section of a developed gonad surrounding the digestive tract. D) Sagittal section showing a highly developed gonad with intrusions into the foot muscle.

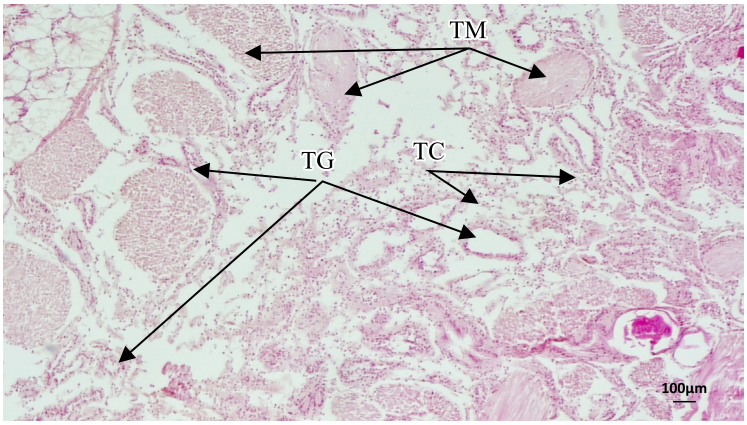

Figure 3. Undifferentiated gonadal stage of *Tagelus adansonii* TC = connective tissue, TG = gonadal tubule, TM = muscle tissue.

(Figure 4 A), with connective tissue occupying most of the gonadal surface.

- Late gametogenesis: as gametogenesis progressed, gonadal tubules enlarged and their walls began to stick together. As a result, follicle cells became less visible. The connective tissue was also greatly reduced. Gonadal tubules contained more oocytes, some of which were stalked or detached from the tubule wall (vitellogenic oocytes). The lumen of gonadal tubules gradually narrowed. At this stage, gonadal tubules were predominantly occupied by gonads and the connective tissue was significantly reduced (Figure 4 B).
- Ripening stage: at this stage, oocytes occupied almost the entire lumen of gonadal tubules. The tubule walls were glued together, with only a few spaces occupied by connective tissue. Tubule size was very large. Vitellogenic oocytes occupied almost the entire lumen of the gonadal tubules (Figure 4 C). At this stage, the size of gonadal tubules was maximal.
- Spawning and renewal stage: this stage was characterized by the presence of large gonadal tubules still attached to each other by their walls. Connective tissue was also visible between the tubules. Walls of gonadal tubules no longer showed a continuous layer of germ cells, but showed free spaces left by the detachment of vitellogenic oocytes (Figure 4 D). Wall of the gonadal tubules contained pre-vitellogenic oocytes, whose development will allow gametogenesis to continue.
- Total spawning and resorption: during this stage, the size of the gonadal tubule decreased considerably and connective tissue took up more space than the tubules. Walls of gonadal tubules were no longer continuous, but crossed each other at certain points. Few vitellogenic oocytes, previtellogenic oocytes and ovogonia were observed in gonadal tubules (Figure 4 E). The space occupied by connective tissue became larger. Gonadal tubules became very small, some with disorganized walls, others containing enucleated, fragmented or degenerated oocytes.

Male reproductive stages were:

- Early gametogenesis: at the start of gametogenesis, gonadal tubules were more numerous and larger than in the undifferentiated phase. Gonadal tubules were more or less diamond-shaped. Within gonadal tubules, sex cells differentiated from the periphery towards the center (centripetally), becoming smaller as they got closer to the lumen (Figure 5 A). The lumen of gonadal tubules was central, rounded and quite wide.
- Late gametogenesis: during late gametogenesis, the tubules were more numerous and contained

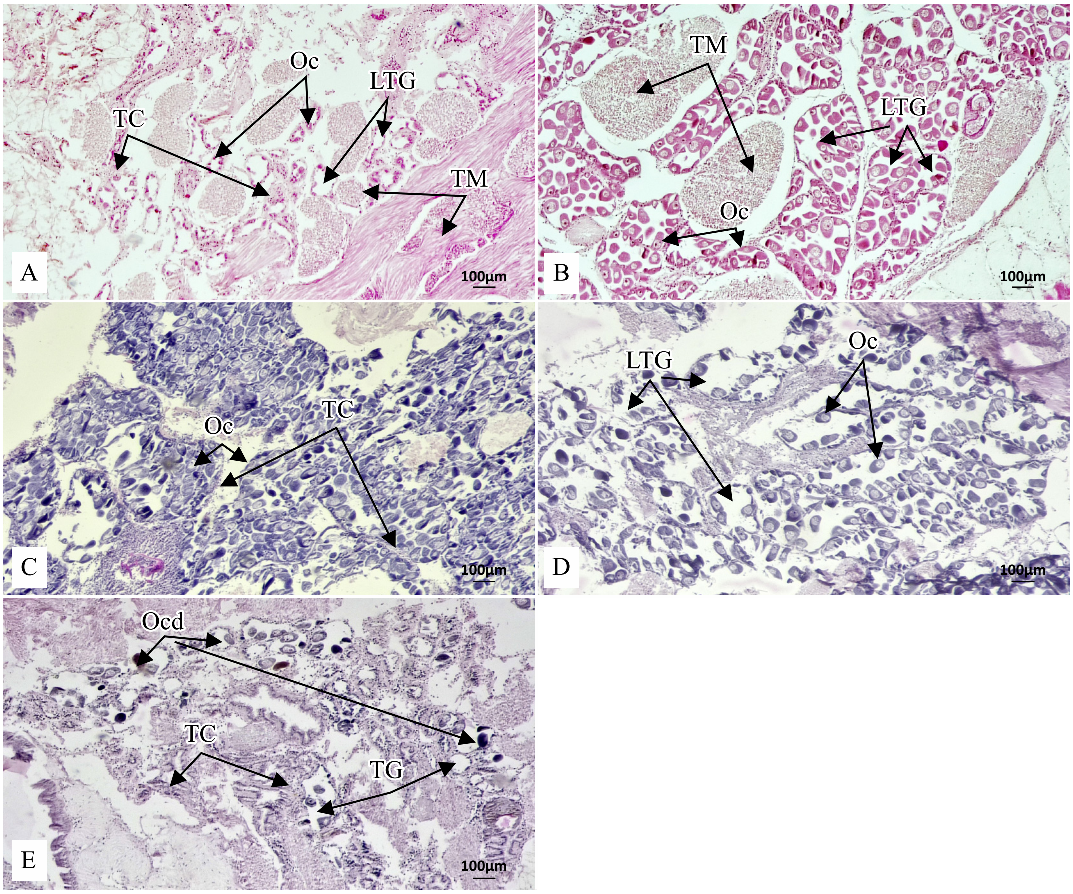

Figure 4. Reproductive stages of female *Tagelus adansonii*. A) Early gametogenesis. B) Late gametogenesis. C) Ripe. D) Spawning and renewal. E) Total spawning and resorption. TC = connective tissue, TG = gonadal tubule, Ocd = degenerating oocyte, LTG = lumen of gonadal tubule, TM = muscular tissue, Oc = oocyte.

more germ cells. Gonadal tubules were also larger and the inter-tubular space was much smaller. The tubule lumen appeared as a white dot or line. Most advanced sex cells (spermatids, spermatozoa) were visible near the lumen (Figure 5 B).

- Ripening and spawning: tubules reached maximum size and follicles adhered to each other. The lumen of gonadal tubules appeared as multiple white lines, giving them a more or less square appearance (Figure 5 C). There was nearly no connective tissue between tubules.
- Total spawning: gonadal tubules no longer had a well-defined shape, but rather a disorganized appearance with dense areas (germ cell islands) and clear areas (lumen). Connective tissue was abundant. Germ cell islands were scattered (Figure 5 D).

In the only case of hermaphroditism noted in this study, the male and female gonadal tubules were clearly distinct.

Observation of gonads confirmed that *T. adansonii* is a gonochoric species. A single case of hermaphroditism was observed in February 2020. In addition to individuals with male or female gonads, there were also individuals with undifferentiated gonads (Figure 6). The total percentage of males was 53.0% (176 individuals), while females ac-

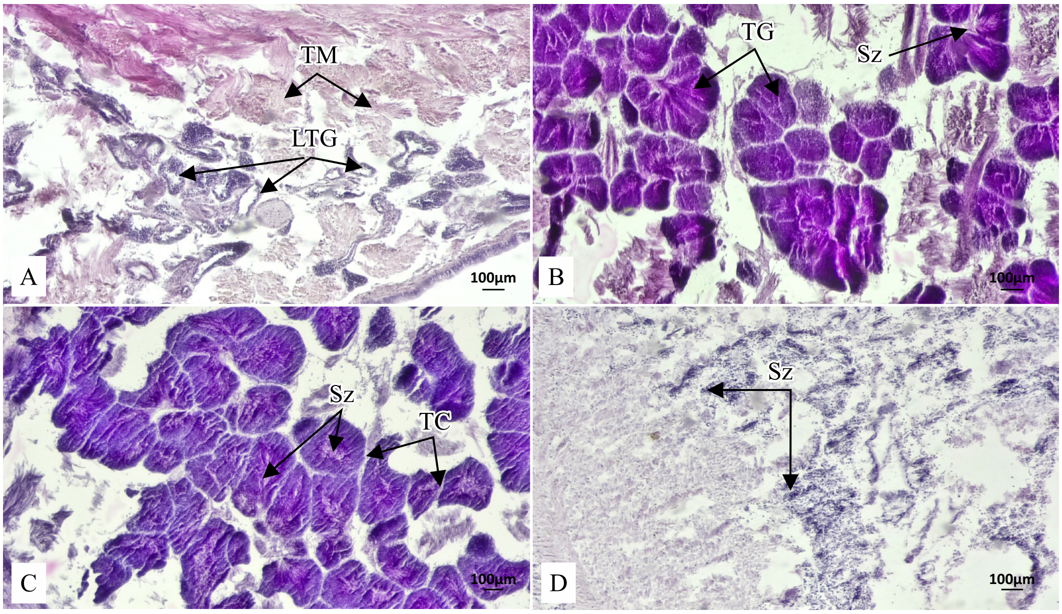

Figure 5. Reproductive stages of male *Tagelus adansonii*. A) Early gametogenesis. B) Late gametogenesis. C) Ripe and spawn. D) Total spawning. TC = connective tissue, LTG = lumen of gonadal tubule, TG = gonadal tubule, TM = muscle tissue, Sz = spermatozoon.

counted for 47.0% (156 individuals). The sex ratio was 1.13:1 for males, but it was not a significant difference (Chi^2 = 0.86787, df = 1, p = 0.3515). The undifferentiated stage was zero between June and December 2019 and May 2020. This stage peaked in February 2020 at 32.0%. The early gametogenesis stage had three peaks, the highest in May 2019 (48.3%) and the other two in January and April 2020 (30.0% and 33.3%, respectively). This stage was not observed between July and October 2019. The late gametogenesis stage showed two peaks in June (44.4%) and November (37.0%), but it dropped to zero in February 2020. The maturation and spawning stage reached high percentages of abundance between July and November 2019 and in May 2020. Its abundance percentage was low in May 2019 and between December 2019 and April 2020. The total spawning stage peaked in December 2019 (Figure 6). The total spawning stage was observed throughout the sampling period, with a low percentage abundance between May and September 2019 (3.3%) and a high percentage in December 2019 (61.5%). The total reproductive stages followed the same trend for both males and females (Figure 7).

Heller (1993), who studied hermaphroditism in bivalves, reported occasional cases of hermaphroditism are found in families such as Arcidae (genus *Anadara*), Unionidae (e.g. *Anodonta*), Mytilidae (*Perna*, *Modiolus* and *Mytilus*), Myidae (*Mya*), Pectinidae (*Placopecten*) and Mactridae (*Spisula*). Additionally, Ceuta et al. (2010) found hermaphroditism in *Tagelus* species, a fact which had not been reported elsewhere. They concluded that it occurs occasionally and could be related to conditions such as parasitism, salinity variation or the presence of pollutants in the environment. Our results evidenced a sex ratio in favor of males (1.13:1), a trend also found in *T. plebeius* (1.06:1) by Ceuta and Boehs (2012). In contrast, Flores and Licandeo (2010) discovered that females dominated in two species of burrowing bivalve mollusks from Ecuador, *Anadara tuberculosa* and *A. similis*, with sex ratios of 2.57:1 and 2.60:1, respectively.

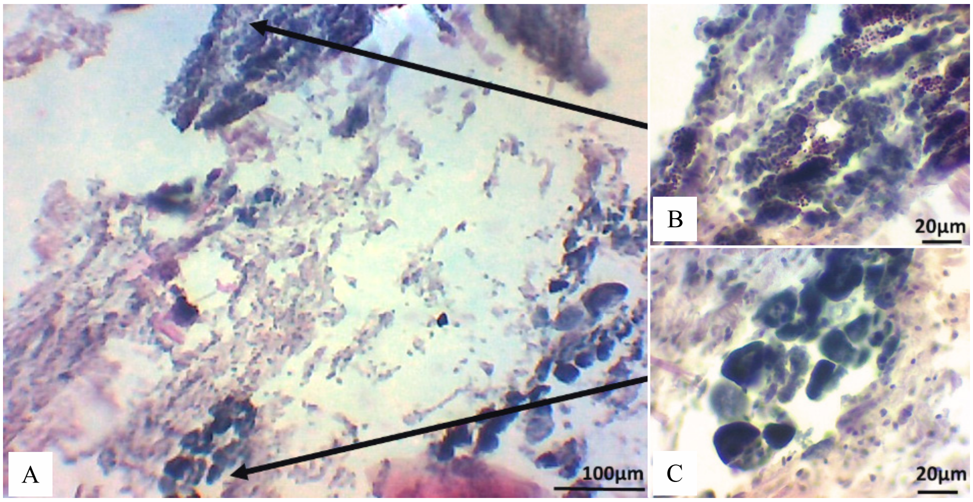

Figure 6. Hermaphroditism stage of *Tagelus adansonii.* A) Hermaphroditism. B) Enlargement of the male part stage ripe and spawn. C) Enlargement of the female stage spawning and renewal.

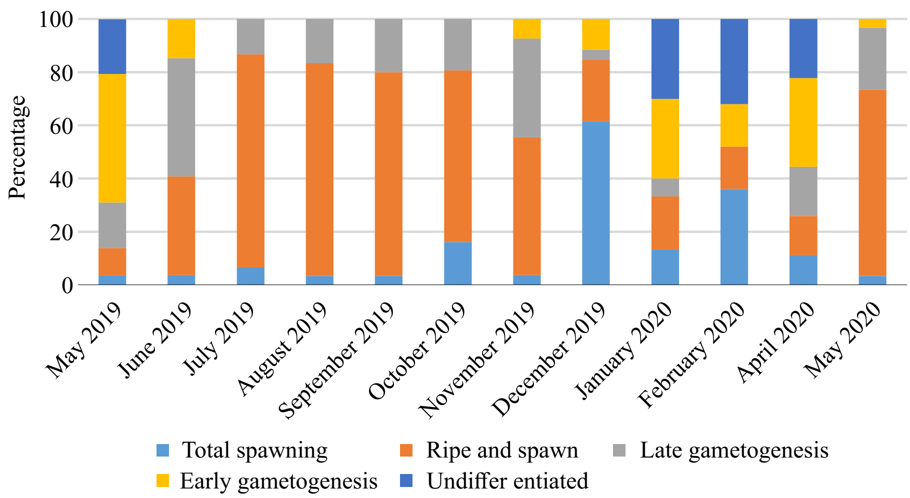

Figure 7. Overall percentage of abundance of breeding stages of *Tagelus adansonii* from May 2019 to May 2020.

We can confirm that reproduction in *Tagelus* may or may not be continuous depending on the location and the species. For example, in *T. plebeius*, gametes are released throughout the year in Brazil (Ceuta 2007; Farias and Rocha-Barreira 2017), whereas reproduction is periodic in Argentina (Cledón et al. 2004). Brazil is a predominantly tropical country and part of its coastline is also subject to upwelling. Studies carried out have shown that latitudinal variations in temperature and seasonal rainfall in the northeast influence the reproduction of *T. plebeius* on the Brazilian coast. This reproductive pattern is characteristic of tropical areas, where species develop opportunistic strategies to produce gametes using energy directly from their diet, rather than energy stored in their body tissues (Freites et al. 2010). Furthermore, the population of *T. plebeius* shows periodic reproductive activity in Argentina (a temperate country subject to upwelling), with gamete development occurring in spring (Cledón et al. 2004). Reproduction is also discontinuous in the population of *T. divisus* from Biscayne Bay, Florida (USA) (Fraser 1967). Farias and Rocha-Barreira (2017) hypothesized that the difference in gamete release duration (continuous or seasonal reproduction) in *T. plebeius* in Brazil and Argentina could be explained by temperature differences. According to our results, the proportion of individuals in the maturation-spawning stage appears to be related to variations in water temperature, salinity and nutrient richness. Domain's (1980) classification of hydric seasons affecting the Senegalese coast shows that the period of maximum gamete emission of *T. adansonii* in this study (July and August) corresponds to the warm season. The upwelling season on the Senegalese coast lasts from January to May (Ould Sidi 2005). During the upwelling season, waters are rich in nutrients (phytoplankton and zooplankton), which makes this period favorable for the accumulation of reserves, especially for species that feed exclusively on plankton. This is also the period when water temperatures are at their lowest for the year (Ould Sidi 2005). June corresponds to a period of transition between cold and warm water. July to October is the warm water period and also the time for rainfalls, which leads to a decrease in salinity. According to Ndong (2003), the rainy season in the Thiès region is between August and October. The period of maximum gamete release appears to be between the end of the upwelling season and the beginning of the warm season. This suggests that a combination of food availability and variations in temperature and salinity are the factors most conducive to gamete emission. Indeed, in some bivalves, food can increase gamete fertility and quality (Utting and Millican 1997), while temperature plays a role in germ cell maturation and spawning initiation (Fabioux et al. 2005).

The reproduction of bivalves in controlled environments depends on several external factors, including temperature, food, salinity and photoperiod. Temperature appears to be a key factor, as the induction of oviposition in controlled environments in mollusks is achieved by a process involving thermal shock (Gerard 1998). The early gametogenesis stage of *T. adansonii* in May and April 2020 was very important, which leads us to believe that the amount of nutrients and temperature are the two main factors in the massive triggering of gametogenesis. It is possible that the high gamete release in May 2020 is the consequence of an early rise in temperature. The length of the reproductive cycle and the number of cycles during the year can be population-specific and vary according to geographical region (Eversole 1989). Particularly, in Senegal, the reproductive period of two bivalve species (*Senilia senilis* and *C. gasar*) is often correlated to the rainy season (Diouf et al. 2009; Sané et al. 2023), as if decreasing salinity were the main factor triggering the massive release of gametes. In our study, however, massive gametes release can be observed as early as May.

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Author contributions

Jeanne E. Diouf: conception; data acquisition; data analysis; writing. Babacar Sané: revision; writing. Ephigenie N. Dione: revision; writing. Malick Diouf: conception; data acquisition; data analysis; revision; validation.

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