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Histological Study of the Sex Ratio and Reproductive Cycle of the Mangrove Oyster *Crassostrea tulipa* (Lamarck, 1819) in the Saloum Delta (Senegal)

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Summary

The mangrove oyster *Crassostrea tulipa* has considerable socio-economic value in Senegal, as in many other West African countries. To better understand its biology, the objective of this study was to determine the sex ratio and the evolution of gonadal development stages of oyster populations in the Saloum Delta. To this end, a monthly sampling of 30 oysters between 34.19 mm and 96.68 mm height was carried out between January 2021 and January 2022. The part of the flesh that encloses the gonads was removed and fixed using Davidson's solution. After dehydration, paraffining and inclusion of the materials, 7 µm thick sections were made using a microtome. These sections were stained with Haris's hematoxylin and eosin and the slides were observed under an optical microscope (Olympus BX41 microscope).

The results showed a predominance of females over males, with a sex ratio of 1 in 2.85. The results also revealed that reproduction was continuous over the year and that spawning was asynchronous: Individuals at the spawning stage were more frequent in the warm season. These results will contribute to a better management of natural stocks and to improve oyster farming.

Keywords: *Crassostrea tulipa*, sex-ratio, reproductive cycle, Saloum delta

1. Introduction

In oysters of the genus *Crassostrea*, reproduction is closely linked to seasonal variations in environmental characteristics such as food availability, temperature and salinity. The reproductive cycle varies depending on the biogeography of oyster species (Antonio *et al*., 2021; Gomes *et al*., 2014). It is more contrasted in temperate zones than in tropical environments (Gomes *et al*., 2014). Several studies have shown that oysters reproduce once a year in temperate zones, usually in spring, when the temperature rises (Ezgeta-Balić *et al*., 2020; Gomes *et al*., 2014; Rayssac *et al*., 2012). In contrast, in the tropics, studies conducted in Brazil have shown continuous reproduction (Antonio *et al*., 2021; Lenz and Boehs, 2011; Nascimento and Lunetta, 1978).

In mangroves of Senegal and the West African sub-region, the indigenous oyster species is *Crassostrea tulipa* (Lapègue *et al*., 2002; Zabi and Le Loeuff, 1992). It has been exploited for centuries and now plays an important role in the economy and nutrition of island and coastal communities (Thiao, 2024; Mahu *et al.*, 2022). With the increase in demand in the market, the pressure on this resource has become very strong. This results in a decrease in natural stocks but also in the degradation of mangrove roots (Thiao, 2024).

Faced with this situation, it is important to put in place effective harvest management measures and develop oyster farming as an alternative. To achieve these goals, the first step is to acquire more information in relation to the biology, reproduction and breeding of the species. The objective of this study was to determine the sex ratio and the temporal evolution of gonadal development stages of oyster populations in the Saloum Delta.

2. Materials and Methods

2.1 Study Area

This study is carried out in the commune of Dionewar located in the Saloum delta, in the Fatick region of central-western Senegal (Figure 1) where the socio-economic life of the communities is essentially based on fishing and shellfish gathering (De Morais, 2011; Fall, 2009). It is an area covered by forests where large populations of *Crassostrea tulipa* grow on the roots of mangrove trees.

Included in the Sudano-Sahelian domain, this zone is also characterized by tropical thermal and water regimes (Sarr, 2009). It is characterized by a cold season (January-May) and a rainy hot season (July-October), separated by transition periods (cold-hot in June ; hot-cold between November and December) (Zabi and Le Loeuff, 1992).

The oysters used for this study were collected at three stations in the mangrove: S1 (13°56.253'; 016°40.867'), S2 (13°51.792'; 016°43.003') and S3 (13°51.125'; 016°44.209') (Figure 1).

Figure 1. Location of sampling stations in the commune of Dionewar (Saloum Delta, Senegal, West Africa)

2.2 Sampling, Biometry and Histological Treatments

The oysters used for this study were collected from the roots of mangrove trees. Each month, from January 2021 to January 2022, 30 individuals with sizes between 34.19 mm and 96.68 mm were collected, for a total of 390 individuals.

In the laboratory, each individual was weighed with a 0.01 g precision electronic scale and the height of its shell measured using a 0.01 mm precision digital and automatic caliper. The soft bodies of the oysters were removed from the shells and wiped with paper towels. The gonadal region was dissected and fixed with Davidson's solution for 48 h. Then, the sections were stored in 70% ethanol until they were further processed.

The materials were subsequently dehydrated by successively soaking them in a series of alcohol baths and incorporated into paraffin. The paraffin blocks were sectioned to a thickness of 7 µm with a Leica hand-held microtome and stained with Harris's hematoxylin, then eosin and mounted on glass slides with EUKITT resin.

To determine the sexes and gonadal development stages of the samples, all slides were examined under an optical microscope (Olympus BX41 microscope) with a computer-connected camera. Photomicrographs of gonads at various stages of development were performed using CMEX-5 Pro software (model 45B2.0).

2.3 Determination of the Sex-Ratio

Sampled individuals were classified according to gamete type. The gonads contain sperm cells for males and oocytes for females. In cases when the gonads contain both oocytes and spermatozoa, individuals were classified as hermaphrodites. Oysters were considered indeterminate in cases where no reproductive cells were found in the gonads. The percentage of each of these categories was calculated relative to the number sampled.

The sex ratio (*SR*) used to compare the number of males to the number of females in the population was determined using the following formula :

$$SR = M / F$$

Where M is the number of males and F is the number of females.

Finally, a sex-based distribution of samples was established to assess the relationship between oyster size and sex.

2.4 Determination of Gonadal Development Stages

The methodology used to classify gonadal development stages was based on that of Barman *et al.* (2022), Ramos *et al.* (2014) and Legat *et al*. (2020). This classification is mainly based on the following criteria:

- the presence, size and position of the follicles;
- the quantity and predominant stage of gametes in the follicles;
- the thickness and appearance of the follicular walls;

- whether or not the intrafollicular spaces (lumen) are occupied;
- the amount of connective tissue in the interfollicular spaces.

3. Results and Discussion

3.1 Results

3.1.1 Sex-ratio

Microscopic analyses of gonadal tissues showed that 24.61% of the samples (96 individuals) were males and 70.26% (274 individuals) were females. No hermaphrodite individuals were found. Oysters of indeterminate sex comprised 5.13% of the samples (20 individuals). For each case, the average values of shell height and oyster fresh weight are given in Table 1.

Table 1. Number of oysters measured, shell height (mean ± standard deviation) and fresh weight (mean ± standard deviation)

Biometric	Sex			
	Males	**Females**	**Indeterminates**	**Total**
Number	96	274	20	390
Shell height (mm)	56.94±12.31	61.49±8.77	55.18±8.63	60.21±9.73
Fresh weight (g)	20.46±10.13	26.06±11.12	20.95±6.73	24.66±10.93

Overall, the calculated sex ratio was 1/2.85, indicating a predominance of females over males. Specifically, a male/female balance was observed once, in January 2021, and one sample consisted entirely of females in August 2021 (Figure 2). In all other months, females outnumbered males (Figure 2).

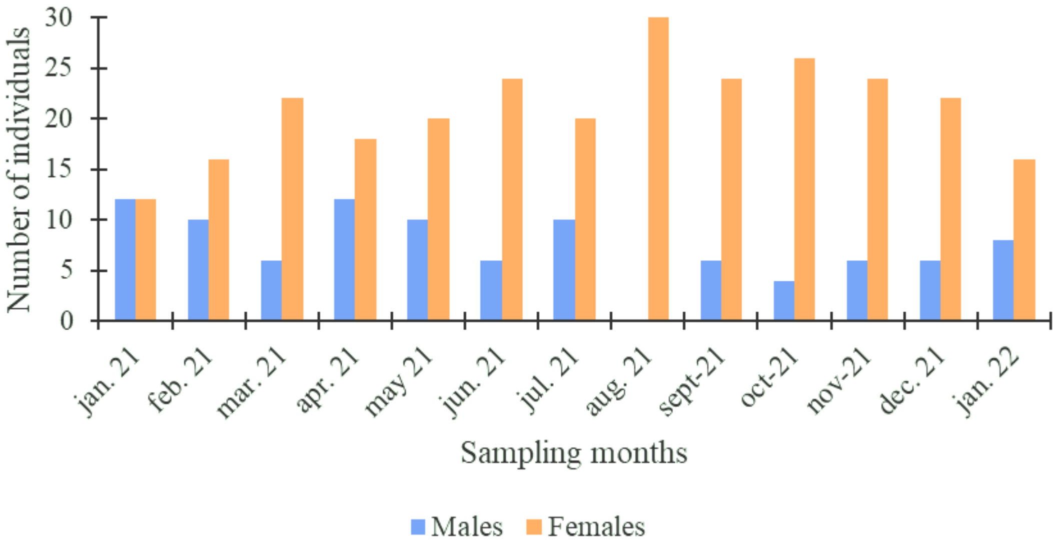

Figure 2. Monthly change of sex ratio in the sampled population

When analyzing the sex ratio distribution by size class, it appears that more than 80% of the males sampled during the 13 months had sizes ≤ 60 mm compared to 56% of the females (Figure 3). Conversely, oysters larger than 60 mm accounted for 44% of females and 19% of males (Figure 3).

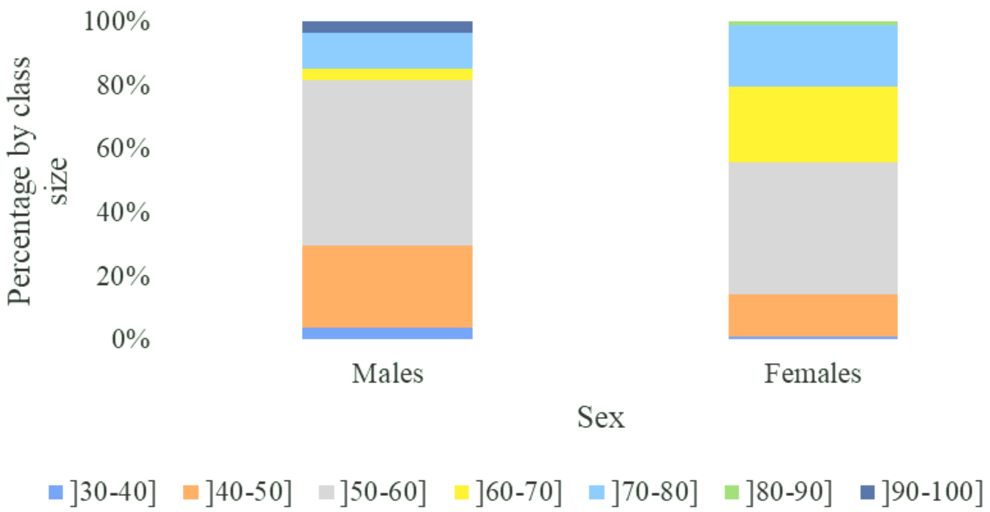

Figure 3. Size class distribution of males and females in the samples

3.1.2 Development Stages and Reproductive Cycle

Analysis of gonadal tissues revealed four stages of development in both males and females. These stages are described in Table 2 and include gametogenesis (stage I), maturation (stage II), spawning (stage III), and reabsorption (stage IV).

Table 2. Description of gonadal developmental stages in the reproductive cycle of males and females of C. tulipa

Stage	Male	Female
Gametogenesis (Stage I)	Follicular walls not juxtaposed; empty central light; presence of germ cells near the inner walls of follicles; thicker follicle walls; Reduction of inter-follicular connective tissues.	Follicular walls not juxtaposed; few oocytes observed, composed of different sizes; thicker follicular walls (presence of oogonia); empty intrafollicular spaces; Presence of significant interfollicular tissue
Maturation (Stage II)	Follicular walls juxtaposed and inconspicuous; high concentration of spermatozoa in the central lumen; reduced connective tissue; reduced interfollicular spaces.	Follicular walls juxtaposed; well-differentiated oocytes, in large numbers and occupying the central lumen of the follicles that increase in volume; narrowed interfollicular connective tissues; reduced interfollicular spaces.
Spawning (Stage III)	Spermatozoids expelled from the follicle; follicle partially empty; broken appearance of walls; little presence of interfollicular connective tissue; intra-follicular and inter-follicular void spaces.	Irregularly shaped follicular walls; follicles with free oocytes in the lumen; presence of oocytes in the drainage ducts; little connective tissue; Appearance of intra-follicular and inter-follicular voids.
Reabsorption (stage IV)	Disorganization of follicles; Spermatozoids remnants in collapsed follicles.	Completely collapsed follicles with a remnant of unexpelled oocytes (apoptosis); Appearance of connective tissue between follicles.
Rest (stage 0)	High presence of connective tissues; absence of follicles and gametes	

These stages are further illustrated in the photomicrographs shown in Figures 4, 5 and 6.

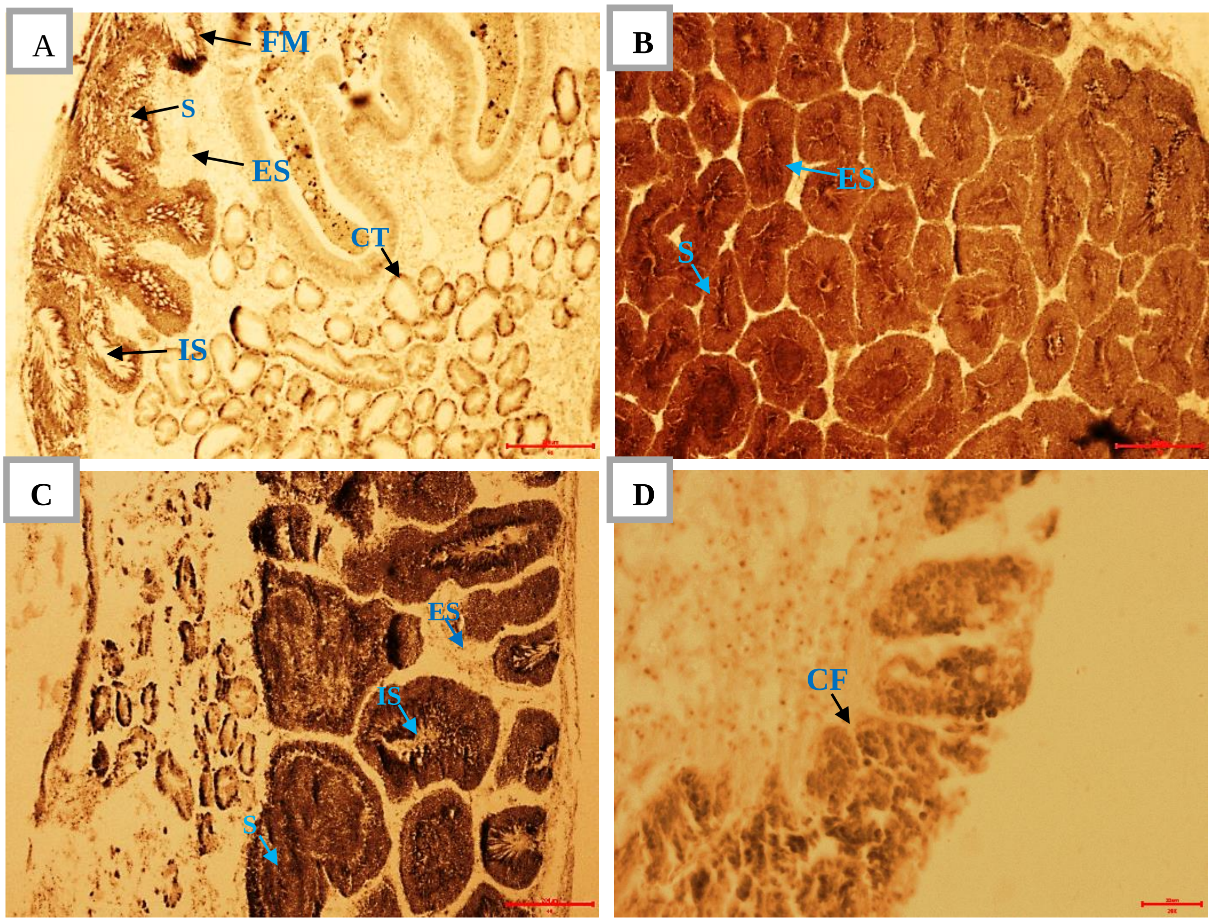

Figure 4. Photomicrographs of gonadal tissue development stages in the male of Crassostrea tulipa. A: Gametogenesis; B: Maturation; C: Spawning; D: Reabsorption; S: Spermatozoids; CT: connective tissue; IS: intrafollicular space; ES, extrafollicular space; FM: follicular membrane; CF: collapsed follicle; Scale bar = 200 µm.

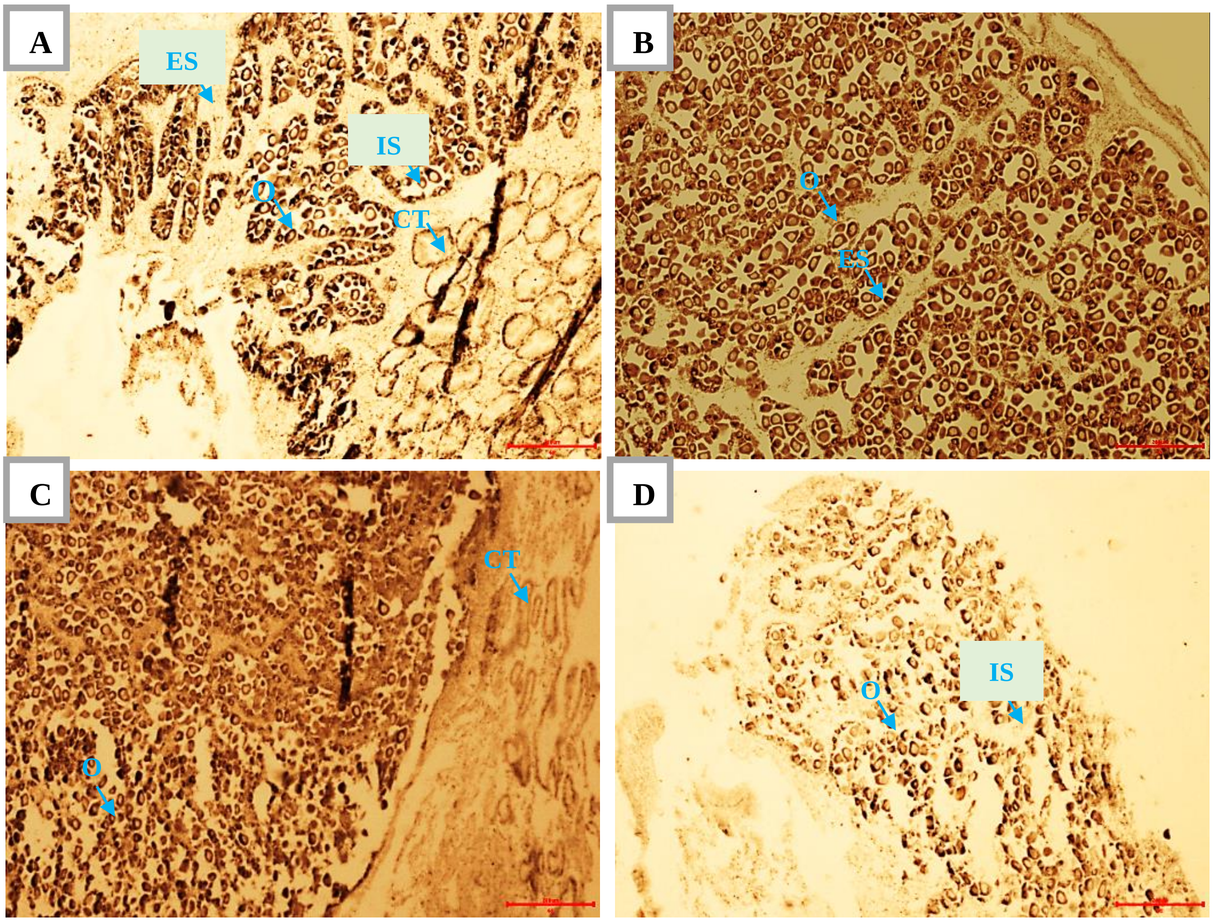

Figure 5. Photomicrographs of gonadal tissue development stages in female Crassostrea tulipa. A: Gametogenesis; B: Maturation; C: Spawning; D: Reabsorption; (CT: connective tissue; IS: intrafollicular space; ES, extrafollicular space; O, oocytes; Scale bar = 200 µm).

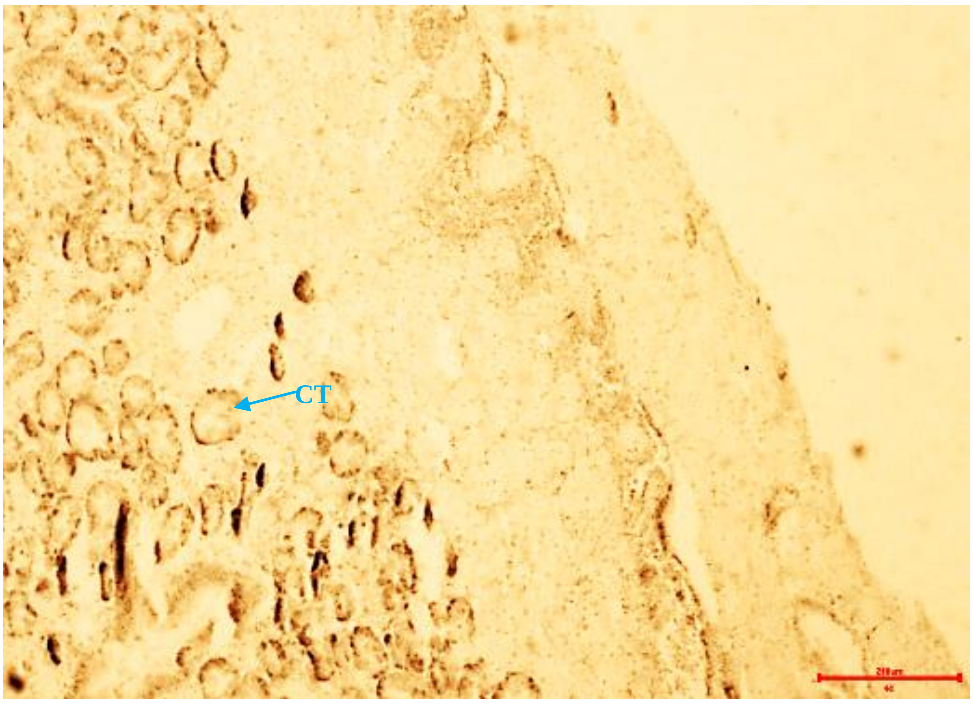

Figure 6. Photomicrograph of the undifferentiated stage. (CT: connective tissue. Scale bar = 200 µm)

When both sexes are combined the results of histological analysis show that, for a given month, the sampled individuals were at different stages of development (Figure 7). In one individual, the gonadal follicles were at different stages of development. This indicates that reproduction is asynchronous at the level of an individual and at the scale of the population.

Gametogenesis was observed during the 13 months of the study with peaks in February and September 2021. The maturation stage was absent only in January 2022 with peaks in March and July. Spawning, which continued throughout 2021, was more marked during the April-November period. Individuals in the reabsorption stage were infrequent, however relatively large proportions were observed in October (20%), December (27%) and January 2022 (27%). Sexual resting was observed in some individuals during the periods January-March 2021 and December 2021-January 2022.

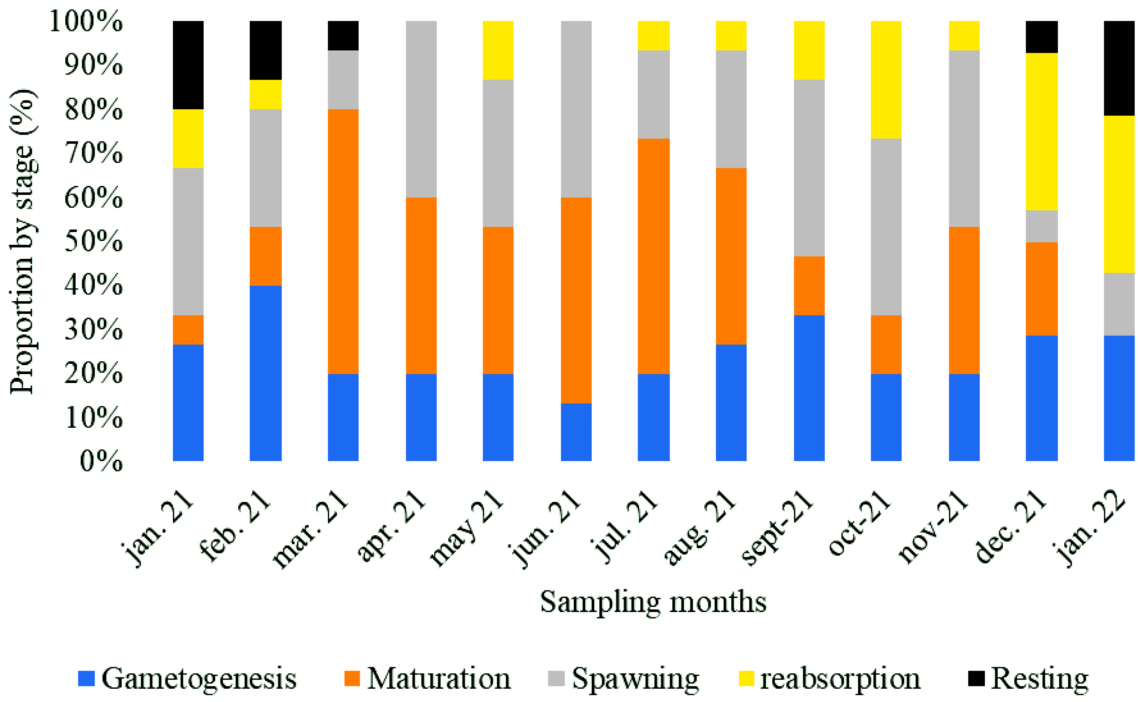

Figure 7. Reproductive cycle of the mangrove oyster C. tulipa in the Saloum delta: Distribution of monthly samples according to gonadal stages

3.2 Discussion

3.2.1 Sex-ratio

An overview of reproductive cycles in bivalves is essential for the sustainable management of fisheries and for the collection of seed from the wild (Barman *et al.*, 2022). The relationship between this biological phenomenon and the variability of physicochemical parameters is also decisive for controlling the factors involved in inducing spawning both in the natural environment and in hatcheries (Gomes *et al.*, 2014; Etchian *et al.*, 2004). Also, as part of effective hatchery management, understanding the sex ratio of the oyster population is fundamental (Barman *et al*., 2022; Lenz, 2008; Etchian *et al*., 2004).

The study of the mangrove oyster population in the Saloum showed a predominance of females over males (SR=1/2.85). These results are similar to those obtained in mangrove areas of Brazil by Legat *et al*. (2020), Ramos *et al.* (2014) and Castilho-Wesphal *et al*. (2015) who worked on *C. tulipa* (Table 3). All these authors found sex ratios in favor of females (Table 3). In terms of gender proportions (Table 3), there are similarities with the results reported by Castilho-Westphal *et al.* (2015) and differences with those obtained by Legat *et al*. (2020).

Table 3. Comparison of results of studies on species of the genus Crassostrea: (N = number of individuals sampled; M = males; F = females; H = hermaphrodites; I = indeterminates; SR = sex ratios; Hm = average height)

Source	Species	Country	N	M (%)	F (%)	H (%)	I (%)	SR (M/F)	Hm (mm)
This study	*C. tulipa*	Senegal	390	24.6	70.3	0	5.1	1/2.85	60.21
Legat *et al.* (2020)	*C. tulipa*	Brazil	260	41.5	55.4	1.2	1.9	1/1.3	42.25
Castilho-Westphal *et al.* (2015)	*C. tulipa*	Brazil	345	26	69	1	4	1/2.7	-
Ramos *et al.* (2014)	*C. tulipa*	Brazil	250	-	-	-	-	1/1.4	42

The slight differences in sex ratio reported in different studies are possibly related to differences in the size of the individuals sampled. Indeed, several studies have shown that oysters of the genus *Crassostrea* are often protandrous; i.e. they mature first as males (Gosling, 2003; FAO, 2019) and the size of first sexual maturity is between 20 and 25 mm (Barman *et al.*, 2022; Galvao *et al.*, 2000), whereas females are markedly dominant in older populations (Broquard *et al.*, 2020; Auby and Maurer, 2004). Indeed, in the present study, most of males (82%) were ≤ 60 mm in size, whereas it was the case for 56% of the females.

The observed differences could also be due to food availability. According to an FAO report (2019), in areas with a good food supply, such as mangrove estuaries, the sex ratio of adult oysters shows a predominance of females, while in areas with low food intake, it is dominated by males. Indeed, studies on other species of the genus *Crassostrea*, (*C. gigas*, *C. saidii*, *C. rhizophorae* and *C. cortezieensis)* have presented results where females were predominant over males (Barman *et al.*, 2022; Antonio *et al.*, 2021; Ezgeta-Balić *et al.*, 2020) whereas Barman *et al.* (2022) reported cases of male predominance or male/female equivalence in species of the same genus. Regarding the consequences of sex ratio on population maintenance, Lenz (2008) believes that a predominance of females is always favorable in the natural population, because, he argues, males can release gametes more frequently than females. This hypothesis is supported by Murua and Saborido-Rey (2003), who believe that the reproductive potential of a species is determined by the number of mature females and their ability to produce viable eggs.

Among the 390 oysters collected for this study, no cases of simultaneous hermaphroditism were observed, contrary to the results of several authors mentioned in Table 3. Considering the proportions of hermaphrodite individuals presented by these authors (between 1% and 2.6%), it seems that the phenomenon is infrequent.

Oysters of indeterminate sex were mainly observed during the cold months (6 out of 30 in January 2021 and January 2022, or 20% of the sample). This period follows the time when spawning was high and gametogenesis was reduced and it probably reflects a temporary exhaustion of the gonads in some individuals, which corresponds to sexual rest.

3.2.2 Gonadal Development Stages: Reproductive Cycle

The small temperature variations in the tropics have been viewed as the main factor responsible for the continued reproductive capacity of *Crassostrea spp.* oysters. (Antonio *et al.*, 2021). Generally, the presence of sexually mature individuals, producing and releasing gametes almost every month of the year is considered as a normal behavior of these oysters (Barman *et al.*, 2022) and a characteristic of the species *C. tulipa* (Galvao *et al*., 2000).

Although spawning frequently occurs year-round in tropical regions (Barman *et al.*, 2022; Antonio *et al.*, 2021; Castilho-Westphal *et al.*, 2015), in some cases it can also be influenced by local fluctuations in thermal amplitude and photoperiod (Rodriguez-Jaramillo *et al.*, 2008), so that temporal variations in gamete maturation occurs among species and even between individuals in the population of the same species (Kennedy and Battle 1964).

The results of the present study showed that during the first 12 months of follow-up (year 2021), sampled populations always included individuals at the spawning stage, which is in line with the results obtained by Barman *et al.*, 2022; Antonio *et al.*, 2021; Castilho-Westphal *et al.*, 2015. The percentages of individuals at the spawning stage were higher during the warm season (Figure 7) when increase in water temperature promotes gamete maturation (Gomes *et al*., 2014). *This relationship is reflected in the occurrence of a significant number of individuals in the maturation stage during the cold-warm transition period (June).*

For some authors, the trigger for spawning is the drop in salinity caused by heavy rainfall during the rainy season (Dawood *et al*., 2023; Barman *et al*., 2022; Gomes *et al.*, 2014; Lenz and Boehs, 2011). *This is not entirely consistent with our results since intense spawning events were not observed, but it* cannot be completely excluded. Indeed, during the rainy season (July – October 2021) some highlights were observed (Figure 7) :

- the proportion of oysters at the ripening stage followed a downward trend from July 2021 (53.33%) to October 2021 (13.33%);
- there was a gradual increase in the total number of individuals in the spawning stage and in the reabsorption stage from 26.67% in July, to 33.33% in August, 53.33% in September and 66.67% in October.

Interestingly, these observations are in line with the results of Gilles (1992) who found more oyster spats on artificial collectors in Casamance during the warm period (July – November) and therefore, some sort of spawning synchronization mechanism during this period is possibly operating.

4. Conclusion

In mangrove oyster populations of the Saloum Delta, female oysters predominate over males, an observation that is consistent with the current view that the species is protandric.

In addition, reproduction occurs all year round, but spawning is more pronounced during the warm season.

These informations are essential for the sustainable management of the resource and the practice of oyster farming, since it helps to target the most favorable period for the collection of spat in the natural environment.

In order to deepen our knowledge on this species, future work should focus on the determination of the first sexual maturity size and on the spatiotemporal variation of larval abundance in the water column, in relation to temperature, salinity and chlorophyll levels.

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Data availability statement

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

Data sharing statement

No additional data are available.

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