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# Reproductive Dynamics of the Razor Clam *Solen marginatus* Pulteney, 1799 (Bivalvia: Solenidae) in Ria Formosa Lagoon

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**Abstract**

The present study describes the reproductive cycle of the razor clam (*Solen marginatus*) from the Ria Formosa lagoon in the Algarve region (southern Portugal), using histological preparations of gonads from samples collected monthly over an 18-month period, from January 2023 to June 2024. Simultaneously, the mean gonadal index (GI) was estimated and its relationship with fluctuations in seawater temperature and chlorophyll *a* concentration was examined. The reproductive cycle of *S. marginatus* showed a seasonal pattern, with a resting period between August and October, followed by the onset of gametogenesis in November, which lasted until March. Ripe individuals were observed between February–March and May, with the spawning period occurring primarily between May and July. The mean GI reflected the temporal variation in the gonadal cycle. Reproduction in this species was strongly influenced by fluctuations in seawater temperature, but was not significantly correlated with chlorophyll *a* concentration. The information gathered in this study is of utmost importance, as it enables the proposal of evidence-based management measures aimed at promoting the sustainable exploitation of this resource. According to these new findings, a closed season (June or July) prohibiting razor clam harvesting in the Ria Formosa lagoon between May and July is proposed.

**Keywords:** gametogenesis; gonad histology; spawning season; mean gonadal index; shellfish harvesting; management measures; closed season

## 1. Introduction

The exploitation of bivalves is a traditional activity of great socioeconomic importance. However, scientific knowledge about the biology of many exploited and commercially valuable species is often scarce [1]. Furthermore, despite the vast ecological and economic importance of marine invertebrates, fisheries targeting these animals are often unregulated, poorly monitored and lack robust scientific assessment [2]. In particular, commercial and recreational bivalve fishing constitutes a cultural, social and economic resource for several coastal communities worldwide [3].

The razor clam *Solen marginatus* Pulteney, 1799 is an infralittoral species that lives buried at shallow depths in sandy or muddy bottoms [4], with a wide distribution throughout the Atlantic Ocean, Black Sea, Mediterranean Sea, North Sea, Baltic Sea and Norwegian Sea [5]. With respect to its harvesting, the species' abundance in intertidal areas, easy capture both by fishery and recreation, and increasing commercial value collectively render it an important economic resource for coastal communities [6]. For this reason, the



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development of fishing and shellfish harvesting activities has raised the need for further research on the reproductive cycle of commercially exploited species in order to implement management measures aimed at promoting the sustainable exploitation of these resources [7].

Only two studies on the reproductive cycle of *S. marginatus* have been carried out in Portugal [6,8]. The Ria Formosa on the south coast of the Algarve is a large (55 km), mesotidal, coastal lagoon with a surface area of approximately 16,300 ha [9]. It is a barrier island system comprising the mainland margin, barrier islands, inlet deltas and the shoreface [10]. A high nutrient availability, intense solar radiation, and a good water exchange driven by tides make this lagoon highly productive [11]. In coastal lagoons like Ria Formosa, food availability is a critical determinant of bivalve reproductive success, with chlorophyll *a* concentration serving as a reliable proxy for phytoplankton biomass that directly influences gametogenic development and spawning synchronization [12]. Conversely, water temperature acts as the primary initiation of gametogenesis [13]. The Ria Formosa represents a valuable socioeconomic resource for the country, driven by activities such as tourism, salt extraction and fisheries [14]. It is particularly prominent in aquaculture, specifically shellfish production, as it is the largest national producer of bivalve molluscs, accounting for approximately 80% of the shellfish consumed in Portugal [15].

In the Ria Formosa lagoon, the razor clam *S. marginatus* has been traditionally harvested using salt as a capture method, both in intertidal and shallow-subtidal areas. In subtidal habitats, the harvesting process is carried out by divers [16]. The use of salt to harvest razor clams is also practised in other European countries, such as Spain [17], Ireland [18], and the UK [19] and can be considered an environmentally friendly method [16]. In 2023, there were 109 licences for the harvesting and commercialisation of razor clams in the area of the Ria Formosa, and 26 professional harvesters officially reported 16,183 kg of catches corresponding to a declared commercial value of €103,810 [20].

The first study on razor clam reproduction carried out in Portugal [8] was based only on macroscopic observation of the gonads. Therefore, there remains a need to conduct a more rigorous analysis of the reproductive dynamics of *S. marginatus* in the Ria Formosa lagoon, where this species constitutes an important economic resource, in order to implement appropriate management measures to ensure the sustainability of the population.

This study aimed to describe the reproductive cycle of *S. marginatus* in the Ria Formosa lagoon, and evaluate the influence of environmental parameters on its reproductive dynamics, based on the fluctuation of the mean gonadal index (GI) throughout the study period. Based on histological analysis of the gonads, the gametogenic development of the target population was compared with that of other populations across its geographical range.

## 2. Materials and Methods

Approximately 30 adult individuals (≥75 mm) of *S. marginatus* were collected monthly by professional harvesters between January 2023 and June 2024 in the Ria Formosa lagoon, off Hangares village of Culatra Island, in the municipality of Faro (Figure 1). The razor clam samples were hand-harvested by divers in apnea using a hypersaline solution as a harvesting procedure. The salt was deposited on the sediment surface above the species' burrowing holes, which induces the emergence of the razor clams to the surface.

In the laboratory, all specimens from each sample were measured for total shell length (SL) and fixed in Davidson's solution for 24 h. The samples were then washed in running water and preserved in 70% alcohol for further processing. After shell removal, the samples were dehydrated using an automatic tissue processor and subsequently embedded in paraffin. The paraffin-embedded blocks were sectioned to 7 μm thick, stained with hematoxylin-eosin and mounted using DPX. Following standard procedures, the histological preparations were subsequently observed under a microscope in order to assign a gonadal maturation stage to each individual. Six stages of the sexual cycle were classified based on the maturation scale previously proposed [17]: Sexual rest (0)—sexes are indistinguishable, follicles and gametes are absent, the gonad is dominated by dense connective tissue; Start of gametogenesis (I)—small follicles emerge within abundant connective tissue, early-stage oocytes (females) or spermatogonia (males) are attached to walls of follicles; Advanced gametogenesis (II)—follicles expand, reducing connective tissue, females show polygonal oocytes, some free in the lumen and others stalked to the walls, males spermatozoa form radial columns toward the centre; Ripe (III)—follicles are maximally distended and filled with gametes, replacing nearly all connective tissue, oocytes are large and spherical/polygonal, spermatozoa are disorganized in the lumen; Spawning (IV)—follicles appear partially or fully evacuated, as follicle diameter decreases, connective tissue is restored and amoebocytes become numerous; Post-spawning (V)—dense connective tissue with occasional residual, isolated gametes (Figure 2).

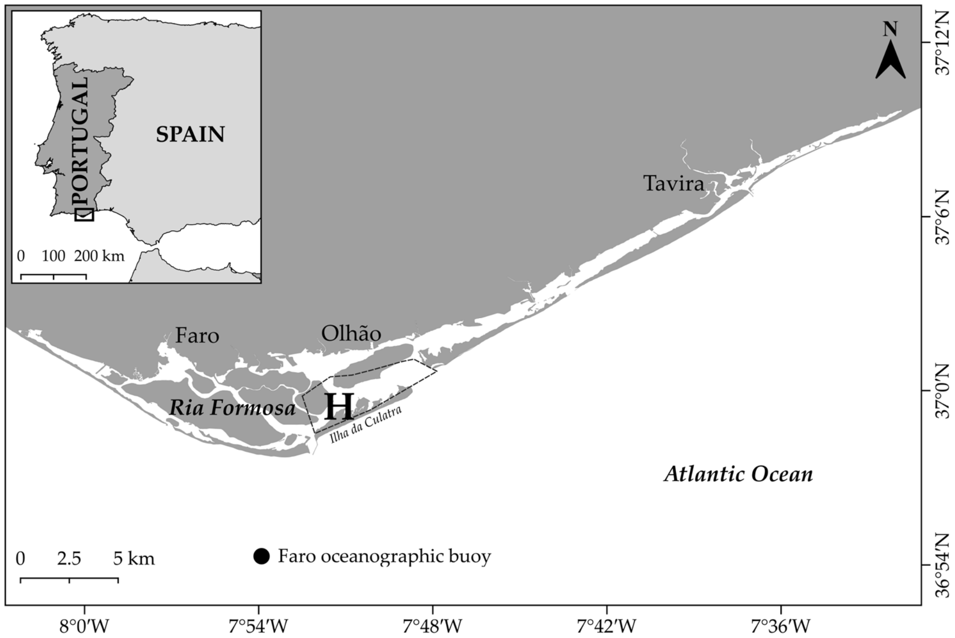


**Figure 1.** Map showing the location of the collecting site for the razor clam *Solen marginatus* off Hangares (H) village of Ilha da Culatra, under the bivalve production area (delimited by the dashed line) in the Ria Formosa lagoon (Algarve coast, southern Portugal).

Data on seawater temperature was recorded during the study period at the Faro oceanographic buoy (36°54.3′ N, 07°53.9′ W) of the Portuguese Hydrographic Institute, which is the closest buoy to the sampling area (Figure 1). Daily interpolated data from satellite observations on average chlorophyll *a* concentration in the seawater (mg/m$^3$) were obtained from the E.U. Copernicus Marine Service Information website, with a resolution of 1 km, for the waters surrounding the sampling site in the Ria Formosa (min lat: 36°58.4′ N; min long: 07°52.8′ W; max lat: 37°01.6′ N; max long: 07°48.4′ W).

To enable the correlation between reproductive effort and environmental parameters, maturation stages were ranked on a numerical scale reflecting gametogenic intensity. Therefore, in order to estimate the GI, previously proposed by Seed [21], the following numerical ranking was assigned to each maturation stage: sexual rest = 0, start of gametogenesis = 3, advanced gametogenesis = 4, ripe = 5, spawning = 2, and post-spawning = 1. The chosen scores clearly show the transition from active spawning (indicated by a sharp decline in IG) to total inactivity.

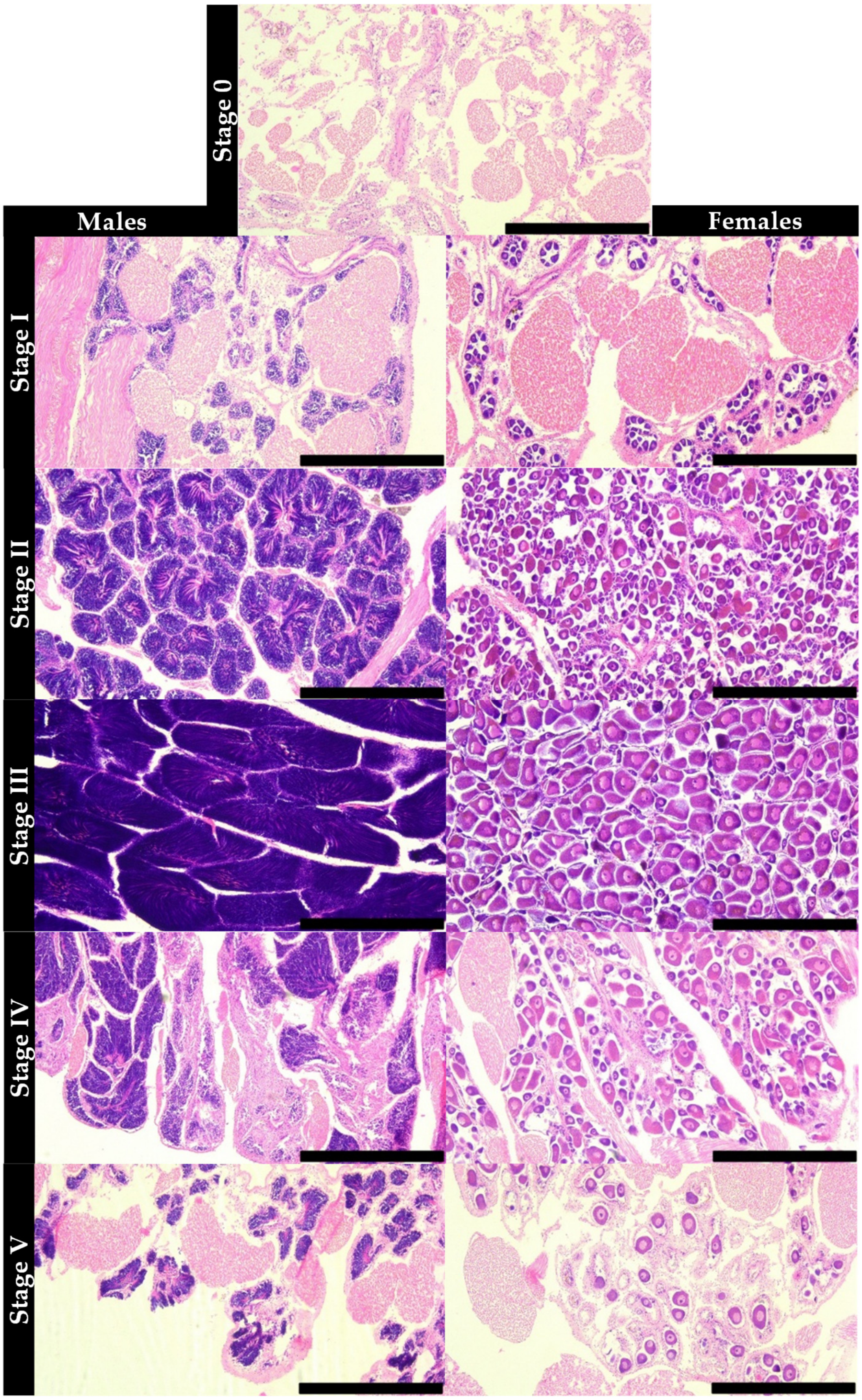


**Figure 2.** Histological sections displaying the stages of gonad development in indeterminate individuals (**centre**), males (**left**) and females (**right**) of razor clams (*Solen marginatus*) in the Ria Formosa lagoon: stage 0—sexual rest; stage I—start of gametogenesis; stage II—advanced gametogenesis; stage III—ripe; stage IV—spawning; stage V—post-spawning. Scale bar = 500 µm.

$$GI = \sum (\text{numbers of individuals at each stage} \times \text{stage ranking})/\text{total number of individuals in each month}.$$

The proportion of the number of males and females in each monthly sample and in the pooled dataset (18 months) was calculated using the chi-square test ($\chi^2$-test) to verify whether the sex ratio differed significantly from the expected 1:1 ratio. The normality of the seawater temperature, chlorophyll *a*, and GI data was assessed using the Shapiro–Wilk test, and the correlation between these variables was subsequently evaluated using Pearson's ($r$) or Spearman's ($\rho$) coefficients, depending on whether the data followed a normal or non-normal distribution, respectively.

Principal component analysis (PCA) was performed to investigate temporal patterns in reproductive condition and environmental variables across the sampling period. The analysis included the gonadal maturation stages (sexual rest, start of gametogenesis, advanced gametogenesis, ripe, spawning and post-spawning) together with environmental descriptors, including chlorophyll *a* and seawater temperature. Variables were standardized (mean = 0, standard deviation = 1) to minimize differences in measurement scales. PCA was conducted using the correlation matrix, and the first two principal components (PC1 and PC2) explained the highest proportion of total variance. Monthly samples were projected onto the PCA ordination space and grouped according to season (winter, spring, summer and autumn). Vector directions and lengths were used to interpret the contribution and correlation of each variable with the principal components. Positive relationships between variables and samples were inferred from similar vector orientations and sample positions within the ordination plot.

Cross-correlation function (CCF) analysis was used to explore potential temporal relationships between environmental variables (seawater temperature and chlorophyll *a*) and the gonadal maturation stages of *S. marginatus*. Cross-correlation coefficients were calculated using Pearson's correlation over a lag range of −6 to +6 months. Negative lags indicate that environmental variables preceded changes in gonadal maturation stages, whereas positive lags indicate that gonadal maturation stages preceded environmental conditions. Statistical significance was assessed using 95% confidence limits under the assumption $\pm 2/\sqrt{n}$, where n is the number of observations.

Data processing and statistical procedures were performed using Microsoft Excel 2016, Statistica (5.1) software packages, and R statistical language [22], and a statistical significance level of $p < 0.05$ was adopted.

## 3. Results

### 3.1. Samples Size and Sex Ratio

*S. marginatus* is a gonochoric species, and no hermaphrodites nor evidence of sex reversal were observed during the present study. A total of 529 razor clams (range = 75.0–132.1 mm SL) were sampled and processed histologically, of which 201 were males (38.0%), 235 were females (44.4%), and 93 were classed as sexually indeterminate individuals (17.6%) (Table 1). During the sampling period, the sex ratio, both in monthly and pooled samples, was statistically balanced between sexes (1.2 F:1 M, $\chi^2 = 2.500$; $p > 0.05$).

**Table 1.** Sex ratio of razor clams (*Solen marginatus*) in the Ria Formosa lagoon.

| Year | Month | M | F | I | % M | % F | % I |
|---|---|---|---|---|---|---|---|
| 2023 | January | 16 | 11 | 3 | 53.3 | 36.7 | 10.0 |
| | February | 14 | 12 | 0 | 53.8 | 46.2 | 0.0 |
| | March | 13 | 17 | 0 | 43.3 | 56.7 | 0.0 |
| | April | 11 | 17 | 0 | 39.3 | 60.7 | 0.0 |
| | May | 12 | 18 | 0 | 40.0 | 60.0 | 0.0 |
| | June | 16 | 12 | 1 | 55.2 | 41.4 | 3.4 |
| | July | 13 | 15 | 2 | 43.3 | 50.0 | 6.7 |
| | August | 3 | 2 | 25 | 10.0 | 6.7 | 83.3 |
| | September | 2 | 4 | 22 | 7.1 | 14.3 | 78.6 |
| | October | 2 | 4 | 24 | 6.7 | 13.3 | 80.0 |

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**Table 1.** *Cont.*

| Year | Month | M | F | I | % M | % F | % I |
|---|---|---|---|---|---|---|---|
| | November | 10 | 12 | 8 | 33.3 | 40.0 | 26.7 |
| | December | 6 | 15 | 8 | 20.7 | 51.7 | 27.6 |
| 2024 | January | 12 | 18 | 0 | 40.0 | 60.0 | 0.0 |
| | February | 11 | 18 | 0 | 37.9 | 62.1 | 0.0 |
| | March | 12 | 18 | 0 | 40.0 | 60.0 | 0.0 |
| | April | 15 | 15 | 0 | 50.0 | 50.0 | 0.0 |
| | May | 17 | 13 | 0 | 56.7 | 43.3 | 0.0 |
| | June | 16 | 14 | 0 | 53.3 | 46.7 | 0.0 |
| **Total** | | **201** | **235** | **93** | **38.0** | **44.4** | **17.6** |

M = male; F = female; I = indeterminate.

### 3.2. Gonad Histology and Reproductive Cycle

A high degree of synchrony was observed in gonadal development, maturation and spawning between males (Figure 3A) and females (Figure 3B), with both sexes displaying analogous temporal patterns in reproductive dynamics throughout the study period. For this reason, we decided to analyze the reproductive cycle of all specimens regardless of sex (Figure 3C).

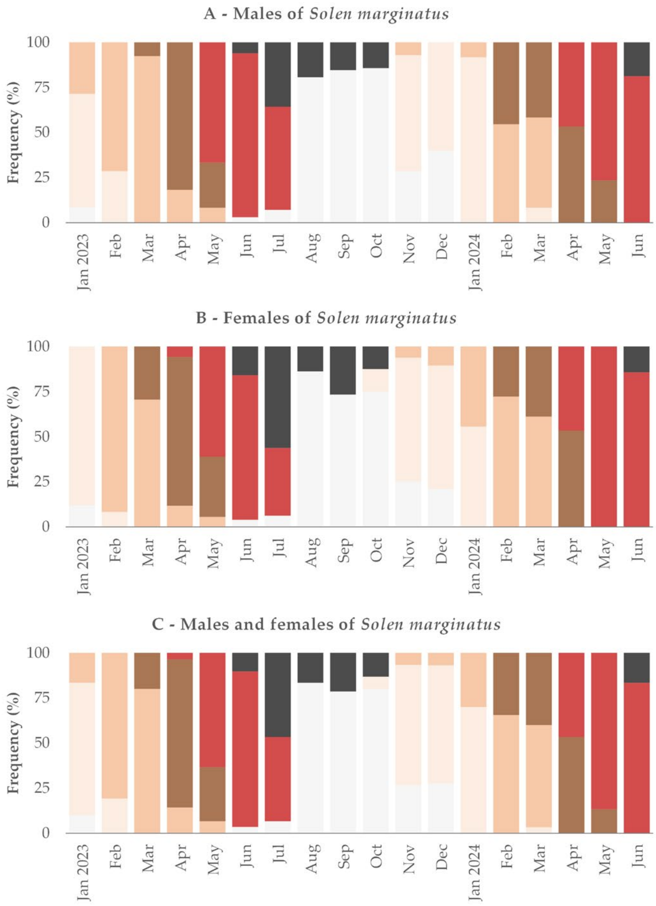


**Figure 3.** Monthly variation in the percentage of each stage of maturation of razor clams (*Solen marginatus*) in the Ria Formosa lagoon ( sexual rest; start of gametogenesis; advanced gametogenesis; ripe; spawning; post-spawning).

The highest percentage of indeterminate individuals, i.e., those in sexual rest, occurred between August and October. Gametogenesis began in November and continued until March. Individuals of *S. marginatus* reached gonadal maturity (stage III) between March and May 2023 and slightly earlier in 2024, with onset in February. Subsequently, spawning occurred mainly between May and July, with approximately half of the individuals spawning in April 2024 (Figure 3C).

### 3.3. Environmental Parameters and Mean Gonadal Index

The highest values of the GI, corresponding to a larger number of individuals in stage III (ripe), were observed in April 2023 (4.75) and March 2024 (4.37). The GI fluctuation observed in Figure 4 corroborated the main trends of the reproductive cycle (Figure 3), with the highest percentage of individuals in stage III occurring in April–May 2023 and in March–April 2024. The lowest GI values (0.17–0.33), corresponding to a higher percentage of indeterminate individuals, occurred between August and October 2023 (Figure 4), coinciding with the resting period observed in Figure 3.

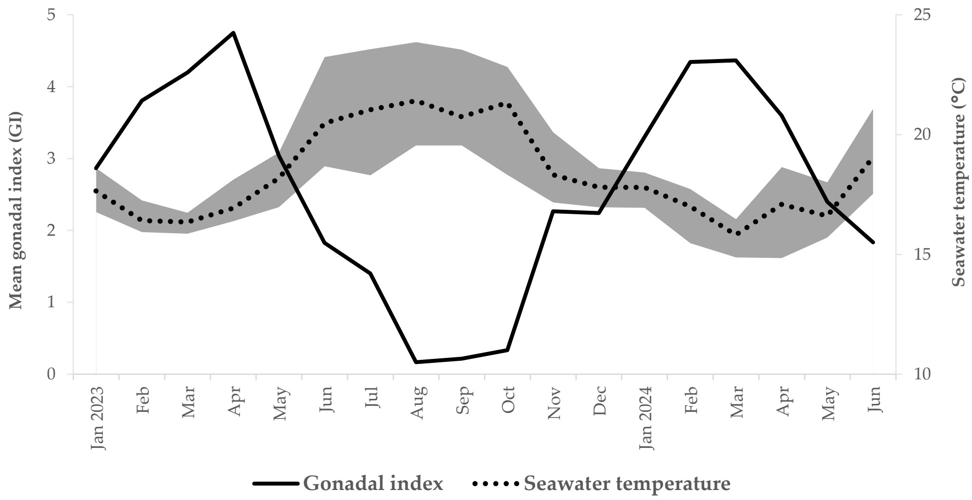


**Figure 4.** Monthly variation in seawater temperature and mean gonadal index of razor clams (*Solen marginatus*) in the Ria Formosa lagoon. The shaded area represents the range between the minimum and maximum seawater temperature values.

The lowest seawater temperature values were reached in March 2023 = 16.4 °C and 2024 = 15.8 °C, matching with high GI values (Figure 4). The maximum seawater temperature peak was reached in August 2023 (mean = 21.4 °C), corresponding to lower GI values, i.e., with the sexual rest period (Figure 3).

A highly significant negative correlation was obtained between the GI monthly variation and fluctuations in seawater temperature ($\rho = -0.903$; $p < 0.0001$). Gonads of *S. marginatus* reached maturity at lower seawater temperatures and subsequently spawned in response to the gradual increase in temperature. Once maximum seawater temperatures were reached, following complete gamete emission, the lowest GI values were recorded, consistent with the resting period.

Chlorophyll *a* concentration in seawater exhibited several fluctuations over the 18-month study period, and reached a maximum of 1.676 mg/m$^3$ in May 2024 and a minimum of 0.509 mg/m$^3$ in January 2024 (Figure 5). However, no significant correlation with mean GI was observed in the present study ($\rho = -0.423$, $p = 0.08$).

PCA revealed a clear seasonal pattern, with gonadal maturation stages and environmental variables jointly structuring the temporal distribution of samples along the first two principal components, which explained 41.4% (PC1) and 23.0% (PC2) of the total variance, respectively (64.4% in total). Samples collected during winter were closely associated with the vectors representing the start of gametogenesis and advanced gametogenesis stages. In contrast, samples collected during spring showed strong associations with the ripe and spawning stages. Summer samples were positively correlated with chlorophyll *a*, post-spawning, and seawater temperature. Late summer and autumn samples clustered in the lower-right quadrant, where the sexual rest vector and higher seawater temperatures had stronger influence. Overall, the PCA highlights the transition from winter developmental stages to spring spawning and ripening phases, followed by inactive summer–autumn conditions associated with warmer seawater temperatures, which reflect a clear annual reproductive cycle (Figure 6).

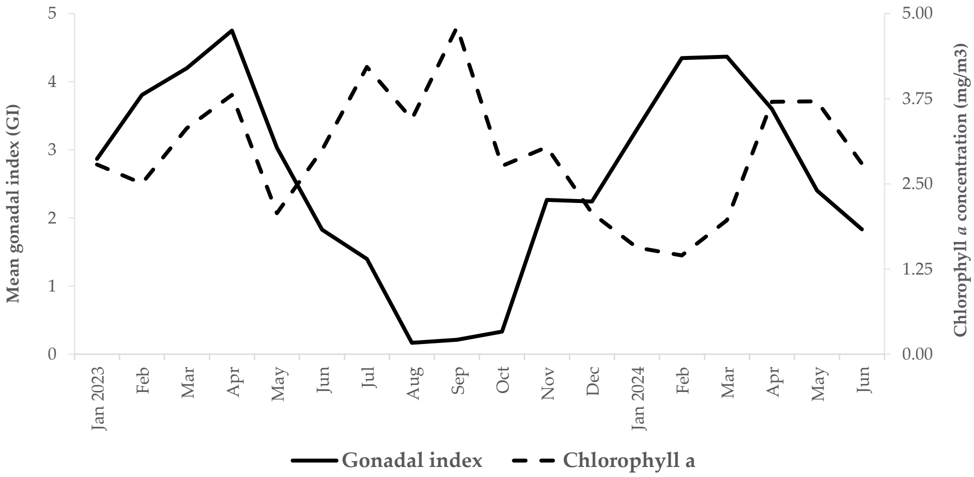


**Figure 5.** Monthly variation in chlorophyll *a* concentration and mean gonadal index of razor clams (*Solen marginatus*) in the Ria Formosa lagoon.

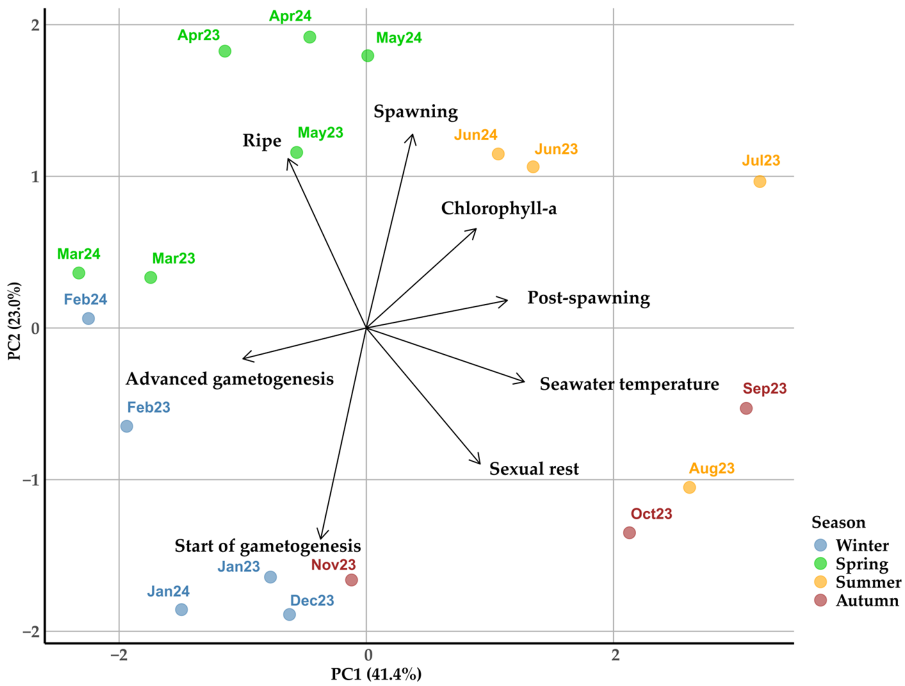


**Figure 6.** Principal component analysis (PCA) showing the temporal distribution of gonadal maturation stages of razor clams (*Solen marginatus*) in relation to environmental variables.

Cross-correlation analysis indicated that seawater temperature and chlorophyll *a* were temporally associated with the reproductive cycle of *S. marginatus*. Early gonadal development showed positive correlations with temperature and chlorophyll *a* at negative lags, suggesting that environmental forcing precedes gametogenesis by several months. In contrast, ripe and spawning stages were negatively correlated with both variables, indicating that maturation and spawning occur following declines in temperature and productivity (Table 2).

**Table 2.** Cross-correlation analysis between environmental variables and the gonadal maturation stages of razor clams (*Solen marginatus*) in the Ria Formosa lagoon.

| Environmental Variable | Maturation Stages | r | Lag (Months) | R | Biological Interpretation |
|---|---|---|---|---|---|
| ST | Sexual rest | 0.792 * | −1 | + | Higher ST precedes sexual rest |
| | Start of gametogenesis | 0.595 * | −3 | + | Higher ST precedes early gametogenesis |
| | Advanced gametogenesis | −0.638 * | 0 | – | Late gametogenesis coincides with lower ST |
| | Ripe | −0.596 * | −1 | – | Ripening occurs following decreasing ST |
| | Spawning | −0.686 * | −3 | – | Spawning associated with lower ST after prior warming period |
| | Post-spawning | 0.767 * | 0 | + | Spent stage coincides with warmer ST |
| Chl | Sexual rest | 0.608 * | −1 | + | Increased Chl precedes inactive stage |
| | Start of gametogenesis | 0.565 * | −4 | + | Chl availability precedes initiation of gametogenesis |
| | Advanced gametogenesis | −0.530 * | −1 | – | Late gametogenesis associated with declining Chl |
| | Ripe | −0.529 * | −2 | – | Ripening occurs after Chl decreasing |
| | Spawning | −0.565 * | −4 | – | Spawning associated with lower Chl following earlier peaks |
| | Post-spawning | 0.535 * | 0 | + | Spent stage coincides with higher Chl |

ST = seawater temperature; Chl = chlorophyll *a*; R = relationship positive (+) or negative (−); r = strongest correlation; * above 95% confidence interval.

## 4. Discussion

The population of *S. marginatus* from the Ria Formosa lagoon (southern Portugal) presented a balanced sex ratio, both in monthly and pooled samples, consistent with a previous report [23]. A sexual resting period of approximately three months (August–October), followed by gametogenesis from November to March, aligns with observations in several Iberian Peninsula populations. In these regions, as observed in the present study, the resting season typically occurs during late summer and early autumn, while gametogenesis consistently extends until March or April (Figure 7). Interannual variability in maturation and spawning seasons was observed in both the studied population and the Aveiro population [6]. A comparison across *S. marginatus* populations suggests a latitudinal gradient, where initiation of spawning occurs earlier in southern regions (e.g., southern Spain and northern Morocco) and is progressively delayed in northern Portuguese and Spanish populations (Figure 7). Razor clam populations in the Iberian Peninsula exhibited shorter spawning seasons than those in Morocco [24] and Tunisia, where a primary spawning event in May was supplemented by partial spawning events between September and December [25].

A highly significant negative correlation was found between seawater temperature and the GI of the population of *S. marginatus* from the Ria Formosa. The monthly variation in GI indicated that gamete release occurred concurrently with the gradual increase in seawater temperature. These findings suggest that the studied population experiences optimal spawning conditions during the rise in seawater temperature, likely anticipating favourable conditions for subsequent larval settlement. Previous studies have demonstrated that increases in seawater temperature and phytoplankton concentration can trigger spawning events before optimal environmental conditions are established [25]. Seawater temperature is known to significantly influence reproductive dynamics [24], a relationship further evidenced by the latitudinal gradient in spawning onset observed across several razor clam populations (Figure 7).

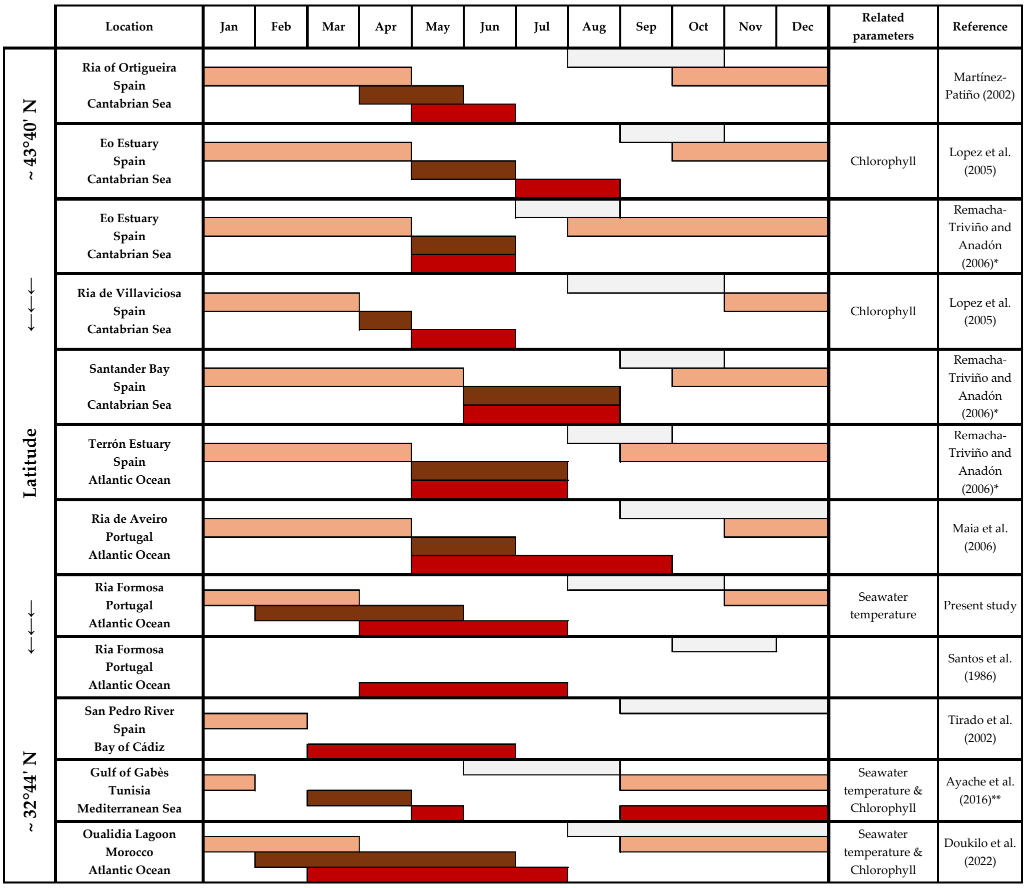


**Figure 7.** Graphical summary of comparison of gametogenic development (■ resting period; ■ gametogenesis; ■ ripe/maturation; ■ spawning) and related environmental parameters described for several *Solen marginatus* populations, ordered from higher to lower latitudes. Martínez-Patiño (2002) [17]; Lopez et al. (2005) [26]; Remacha-Triviño and Anadón (2006) [27]; Maia et al. (2006) [6]; Santos et al. (1986) [8]; Tirado et al. (2002) [23]; Ayache et al. (2016) [25]; Doukilo et al. (2022) [24]. * The authors considered ripe and spawning stages as a single season; ** the authors observed a season with partial spawning events.

Annual reproductive cycles can be influenced by interannual seawater temperature oscillations, which may advance or delay the cycle [28], corroborating the annual difference in onset of spawning of the present study. Differences in the duration of the gametogenic development stages are expected due to both exogenous and endogenous parameters [27].

Environmental variables with the greatest influence on the reproductive cycle of shellfish resources are seawater temperature and food availability [29]. However, in the present study, no significant relationship was found between chlorophyll *a* concentration and variation in mean GI. While some studies report no significant environmental effects on reproduction [23], temperature and food availability are generally considered the key drivers of reproductive timing [24] and energy allocation in bivalves [30]. Interactions between temperature, food availability, salinity and light influence the onset of gametogenesis, maturation and the overall timing of the spawning season [31]. These factors act directly by affecting metabolic rates, or indirectly by promoting the transfer of energy reserves from other organs to the gonad [32].

Currently, there is an increasing need to implement management measures in fisheries that are knowledgeable about local realities and connected to their ecosystem, which requires robust scientific support. Studying the reproductive cycle of commercially exploited marine species can therefore support the establishment of key management strategies, such as a biological closed season, which translates to a temporary ban on harvesting in practice. In the present study, gamete release of *S. marginatus* in the Ria Formosa lagoon was observed between May and July, with maximum spawning intensity between May and June.

This study provides a necessary update to previous research in the Ria Formosa, validating previous macroscopic findings regarding spawning and inactivity periods [8]. By employing histological techniques, we achieved a more rigorous description of gametogenic development, enabling a precise definition of the gametogenesis and maturation phases. To improve the understanding of energy distribution during the gametogenic cycle of *S. marginatus* in the Ria Formosa, future studies should consider incorporating biochemical analyses to complement the histological data presented here. The present study focuses on a single site (Hangares), but it is important to note that the Ria Formosa is a heterogeneous system, where local environmental factors can influence reproductive patterns. Therefore, future research should include multi-site sampling to capture this environmental variability.

A closed season for razor clam harvesting (including recreational harvesting) and commercialisation is recommended for the month following the spawning peak (June or July) in order to ensure the protection of spawning and, most importantly, larvae settlement within this ecosystem.

**Author Contributions:** Conceptualization, P.M.; methodology, P.M.; software, P.M.; validation, P.M., F.P. and A.N.C.; formal analysis, P.M., F.P. and A.N.C.; investigation, P.M.; resources, P.M. and M.B.G.; data curation, P.M., F.P. and A.N.C.; writing—original draft preparation, P.M.; writing—review and editing, P.M., F.P., A.N.C. and M.B.G.; visualization, P.M.; supervision, P.M.; project administration, M.B.G.; funding acquisition, M.B.G. All authors have read and agreed to the published version of the manuscript.

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