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**Reproductive dynamics, gametogenic development and hermaphroditism of the
variegated scallop *Mimachlamys varia* in the eastern Adriatic Sea**

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Abstract

The variegated scallop *Mimachlamys varia* (Linnaeus, 1758) has potential for aquaculture diversification in the Mediterranean, but its reproductive biology in the Adriatic Sea remains poorly documented. Scallops maintained in suspended culture in Mali Ston Bay, eastern Adriatic Sea, were sampled over one annual cycle to characterize reproductive dynamics and their relationships with environmental conditions. Gonadal development was evaluated using histology, gonadosomatic index (GSI), condition index (CI), oocyte morphometry and monitoring of seawater temperature, salinity and chlorophyll *a*. Histological overlap among developing, mature, partially spawned and spent gonads indicated a prolonged and asynchronous reproductive cycle consistent with repeated partial spawning. Females exhibited a more distinct seasonal pattern of maturation and spawning, whereas males maintained reproductive activity throughout much of the year. Gonadal maturation occurred mainly during autumn and winter, while partially spawned and spent stages became increasingly frequent from winter to early summer. GSI followed the histological pattern and was negatively associated with seawater temperature, but showed no significant relationship with salinity or contemporaneous chlorophyll *a* concentration. CI displayed a less consistent seasonal trajectory. Hermaphrodites occurred at low frequency across multiple sampling periods, while the smallest sexually differentiated individuals were male, a pattern consistent with protandric sex expression. Compared with some Atlantic populations, the Adriatic population showed a more prolonged and less synchronized reproductive cycle. These findings identify seasonal windows relevant to broodstock collection and provide a biological basis for hatchery conditioning and aquaculture development of *M. varia* in the Adriatic Sea.

Keywords: *Mimachlamys varia*; reproductive cycle; hermaphroditism; gametogenesis; Adriatic Sea; aquaculture

Introduction

The variegated scallop *Mimachlamys varia* (Linnaeus, 1758), formerly classified as *Chlamys varia*, is a small pectinid bivalve distributed along the northeastern Atlantic coast and throughout the Mediterranean Sea. Within European waters, *M. varia* supports regional fisheries and is recognized as a commercially relevant scallop species, although its exploitation and culture remain less developed than those of larger pectinids (Duncan et al. 2016). Interest in the species as a candidate for aquaculture diversification has been supported by its relatively rapid growth, adaptability to suspended culture and potential for production in Mediterranean coastal environments (Antolović and Antolović 2012). In the eastern Adriatic Sea, previous studies conducted in Mali Ston Bay demonstrated favorable growth and survival of *M. varia* under suspended cage-culture conditions, although performance varied with culture depth (Rathman et al. 2017). Despite this aquaculture potential, the annual reproductive cycle, spawning phenology and patterns of sex expression in Adriatic populations remain poorly characterized.

Reproduction is a fundamental component of bivalve life history because the timing and intensity of gametogenesis and spawning directly influence recruitment, population persistence and aquaculture productivity. In scallops, the reproductive cycle comprises gonial proliferation, gamete development, gonadal maturation, spawning and post-spawning resorption and recovery. These processes are governed by interactions between endogenous physiological rhythms and environmental conditions (Gosling 2003; Barber and Blake 2016). Seawater temperature and food availability are among the most influential external factors affecting the rate of gonadal development, the timing of spawning and the accumulation and mobilization of reserves in pectinids (Iglesias et al. 2012; Šebalj et al. 2026). Their effects are not necessarily independent, however, because reproductive development may reflect thermal history, food quantity and quality, physiological condition and the capacity to store and subsequently mobilize nutrients. Reproductive responses to individual environmental variables should therefore be interpreted within the broader seasonal context.

Histological examination provides the most direct assessment of gonadal condition because it permits evaluation of follicular organization, germ-cell differentiation, vitellogenesis, spermatogenesis, gamete release and post-spawning resorption (Davidson and Worms 1989; Barber and Blake 2016). Histology is particularly important for species

exhibiting asynchronous gametogenesis or repeated partial spawning, for which changes in gonad mass alone may not accurately represent reproductive status. Gonadosomatic index (GSI), condition index (CI) and oocyte morphometry can provide complementary quantitative information, but each has limitations when considered independently. GSI reflects changes in relative gonad mass but cannot reliably distinguish between advancing maturation, partial evacuation and residual gonadal tissue. CI provides an indirect measure of physiological condition but does not identify the biochemical substrates supporting reproduction. Oocyte morphometry provides additional information on ovarian development and the coexistence of different oocyte cohorts. Integrating these approaches with histological staging therefore permits a more robust assessment of reproductive dynamics than reliance on any single indicator.

Scallops exhibit considerable diversity in reproductive strategy, ranging from short and highly synchronized spawning periods to prolonged gametogenic activity and multiple spawning events. Extended reproductive activity and repeated partial spawning have been documented in *Argopecten purpuratus*, where reproductive timing varies in relation to regional environmental conditions and large-scale climatic events (Cantillán et al. 2005). Overlapping female gonadal stages have also been reported in cultured *Nodipecten nodosus* (Sühnel et al. 2010). Comparable interactions among environmental variability, physiological condition, energy allocation and gametogenesis have been described in other marine bivalves (Popović et al. 2013; Pérez et al. 2013). Moreover, Adriatic scallop species exposed to broadly similar environmental conditions can exhibit markedly different growth, reproductive and energy-allocation strategies, demonstrating that reproductive phenology is strongly species and population specific (Ezgeta-Balić et al. 2022).

Current knowledge of reproduction in *M. varia* is derived predominantly from Atlantic populations. Shafee and Lucas (1980) described intermittent spawning in the Bay of Brest, including partial spawning followed by renewed gonadal development and subsequent gamete release. On the west coast of Ireland, spawning and settlement varied among years, indicating that reproductive output and recruitment are not temporally fixed within the species (Burnell 1991). Burnell (1995) further described age-related protandry, with smaller and younger scallops functioning predominantly as males and female representation increasing with age and body size. In Galicia, reproductive development

and reserve-storage cycles varied with depth, reflecting differences in temperature and food conditions experienced by the scallops (Iglesias et al. 2012). Collectively, these findings indicate that *M. varia* possesses a flexible reproductive strategy whose expression may vary among populations in response to local environmental regimes. Nevertheless, comparable information is unavailable for the eastern Adriatic Sea. To our knowledge, no integrated histological assessment of the reproductive cycle and hermaphroditism of *M. varia* has previously been conducted in the eastern Adriatic. This knowledge gap is relevant to both population biology and aquaculture because reproductive timing affects broodstock selection, conditioning schedules, spawning induction, hatchery planning and spat collection. The present study therefore aimed to characterize the annual reproductive cycle of *M. varia* maintained in suspended culture in Mali Ston Bay by integrating histological staging, GSI, CI, oocyte morphometry and environmental monitoring. Specifically, the study sought to describe male and female gametogenic development and spawning patterns, assess temporal variation in GSI and oocyte perimeter, examine CI as an indirect indicator of physiological condition, evaluate associations between reproductive indicators and seawater temperature, salinity and chlorophyll *a* and characterize sex composition and the occurrence of hermaphroditic individuals.

Materials and methods

Study area and culture conditions

The study was conducted in Bistrina Cove (42°52' N, 17°42' E), within Mali Ston Bay on the eastern Adriatic coast of Croatia (Fig. 1).

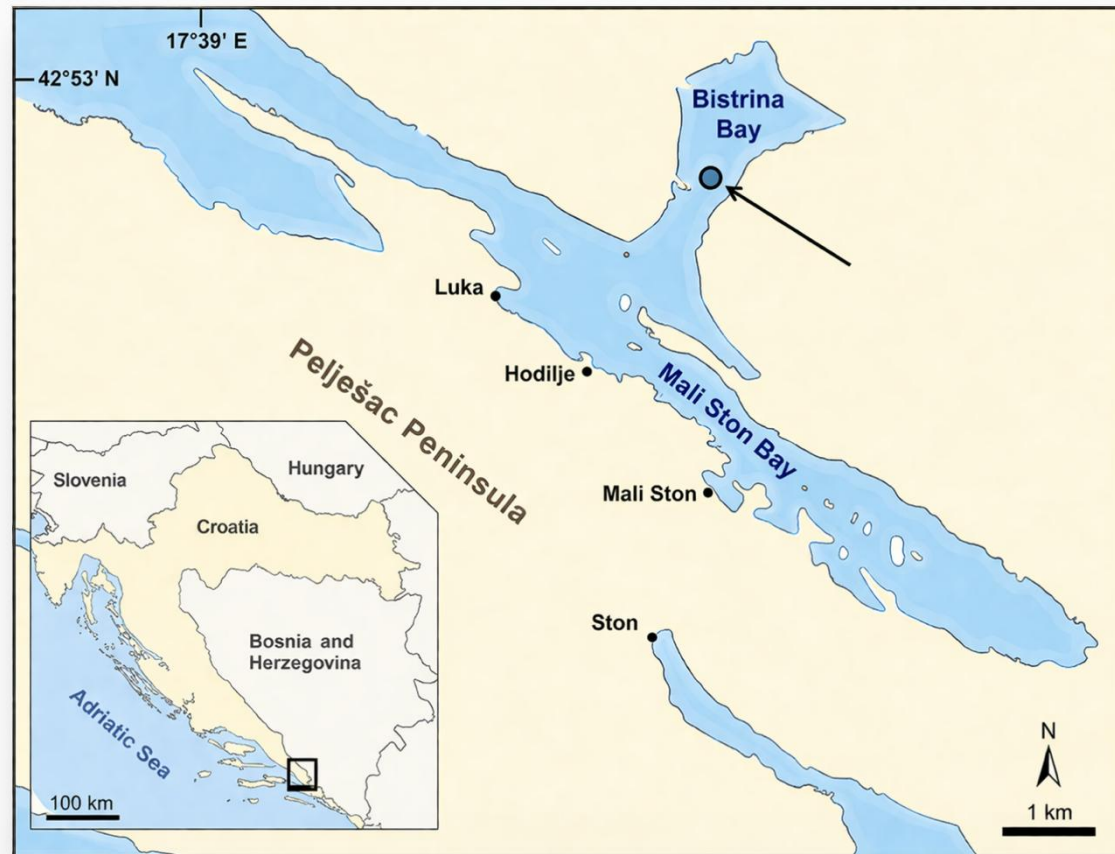


Figure 1. Location of Mali Ston Bay and the experimental farming area in Bistrina Cove, eastern Adriatic Sea.

A cohort of approximately 600 *Mimachlamys varia* was maintained in suspended culture. Scallops were divided between two culture units, each containing approximately 300 individuals distributed among six plastic baskets at an initial density of 50 scallops per basket. Thus, 12 baskets were used in total. The baskets were suspended at a depth of approximately 2 m. Biofouling was removed monthly from the baskets and scallop shells to maintain comparable culture conditions throughout the study.

Sampling and biometric measurements

Sampling was conducted approximately twice monthly over one annual cycle. Two sampling events were generally completed each month, however only one sample was obtained in February because adverse weather prevented the second scheduled collection. Adult scallops were randomly collected from the suspended culture baskets at each sampling date. The number of individuals included in CI, GSI and histological assessments varied among sampling dates (20 per sampling). Additional smaller scallops were collected at selected sampling dates specifically to assess early gonadal

differentiation, sex expression and the minimum size at sexual differentiation. These additional small individuals were included in the histological assessment but excluded from CI and GSI analyses. Shell height and shell length were measured to the nearest 0.1 mm using Vernier callipers. Total wet mass was recorded using a laboratory balance. Each scallop was opened by severing the adductor muscle, after which the soft tissues were removed and the total soft-tissue and gonad wet masses were recorded separately.

Condition index and gonadosomatic index

The condition index (CI) was used as an indirect indicator of whole-animal physiological condition and was calculated as:

$$CI = \frac{W_m}{W_t} \times 100$$

where W_m is the total soft tissue wet mass (g) and W_t is the total wet mass of the individual (g).

The gonadosomatic index (GSI) was calculated as:

$$GSI = \frac{W_G}{W_m} \times 100$$

where W_G is the weight of the gonad wet mass (g) and W_m is soft tissue wet mass (g).

Histological processing and gonadal staging

Gonad samples were removed immediately after dissection and fixed in modified Davidson's solution. A total of 250 scallops, including the additional small specimens collected for assessment of early gonadal differentiation, were examined histologically.

Following fixation, samples were dehydrated through a graded ethanol series, cleared in xylene and embedded in paraffin using an automated tissue processor (Excelsior AS, Thermo Fisher Scientific, USA). Sections of 2 μ m thickness were cut using a rotary microtome (Microm HM 355S, Thermo Fisher Scientific, USA), mounted on glass slides and stained with modified Harris haematoxylin and Young's eosin.

Histological sections were examined by light microscopy at magnifications of 100 $\times$ and 400 $\times$. Digital images were obtained using an Axio Scan.Z1 slide scanner (Zeiss, Germany) and processed using ZEN 2.3 software.

Each individual was classified histologically as male, female or hermaphroditic. A specimen was classified as hermaphroditic when both ovarian and testicular tissues were observed within the same gonadal section. Hermaphroditic gonads were further described as female-dominant or male-dominant according to the relative predominance of ovarian

or testicular tissue. Male and female gonads were assigned to one of six developmental stages: Inactive, early developing, late developing, mature, partially spawned or spent.

Gonadal stages were assigned according to follicular or acinar organisation, the relative abundance and developmental state of germ cells, the amount of interfollicular connective tissue, evidence of gamete release and the presence of residual or resorbing gametes. The classification was based on established histological criteria for bivalves, with modifications reflecting the gonadal organisation observed in *M. varia* (Davidson and Worms 1989; Walker and Power 2004; Barber and Blake 2016). The detailed criteria used for each male and female developmental stage are presented in Table 1.

Oocyte morphometry

Oocyte development was assessed quantitatively in female gonadal sections. Up to 50 oocytes with clearly visible nuclei were randomly selected from each available female section. Oocyte perimeter was measured from digital histological images using ImageJ software, version 1.48, 64-bit.

Individual oocyte measurements were summarised by sampling date to describe temporal variation in oocyte size. Because multiple oocytes were measured within the same female and the identity of the female from which each oocyte originated was not retained in the archived dataset, individual oocytes were not considered independent biological replicates. Consequently, oocyte-perimeter data were interpreted descriptively and no date-level inferential test or post hoc statistical grouping was applied.

Environmental variables

Seawater temperature (°C) and salinity (psu) were recorded daily at the culture depth using a WTW 315i multiparameter instrument (WTW, Weilheim, Germany).

Water samples for chlorophyll *a* determination were collected at each sampling point, at the culture site. Chlorophyll *a* concentration was determined fluorometrically following extraction in 90% acetone according to Strickland and Parsons (1972). Concentrations were expressed as mg m⁻³.

Statistical analysis

Because sample sizes and variances differed among sampling dates, temporal differences in CI and GSI were evaluated using Welch's one-way analysis of variance. When the test was significant, Games–Howell pairwise comparisons were used to identify differences

among sampling dates. Dates sharing at least one superscript letter were not significantly different, whereas dates with no letter in common differed significantly at the family-wise significance level of 0.05.

Relationships between biological indices and environmental variables were assessed at the sampling-date level using Pearson correlation coefficient. Mean CI, mean GSI and mean oocyte perimeter for each sampling date were matched with the corresponding environmental values, thereby avoiding the treatment of multiple scallops or oocytes exposed to the same sampling-date conditions as independent environmental observations.

All statistical tests were two-sided, and statistical significance was accepted at $p < 0.05$. Statistical analyses and graphical presentation were performed using GraphPad Prism version 11.0.

Results

Sex composition and gonadal histology

Among all histologically examined scallops, including additional small individuals selectively collected to assess early sexual differentiation, 112 were male (44.8%), 125 were female (50.0%) and 13 were hermaphroditic (5.2%). Males and females therefore occurred in broadly similar numbers within the examined sample. The smallest sexually differentiated individuals, with soft-tissue wet masses of 0.1–0.5 g, were male. Hermaphroditic individuals occurred at multiple sampling dates throughout much of the annual cycle, although they represented only a small proportion of the total sample.

Gonadal development was classified into six stages according to follicular or acinar organisation, the abundance of connective tissue and the degree of gamete development: inactive, early developing, late developing, mature, partially spawned and spent (Table 1).

244 Table 1 Histological criteria used to classify female and male gonadal stages in *Mimachlamys*
 245 *varia*

Stage	Development phase	Female gonad (oogenesis)	Male gonad (spermatogenesis)
1	Inactive	Undifferentiated gonadal tissue with abundant connective tissue; follicles poorly developed or absent; presence of undifferentiated oogonia.	Irregular and poorly defined follicles; predominance of undifferentiated germ cells; abundant interlobular connective tissue.
2	Early developing	Small oogonia and early germ cells attached to acinar walls; thick follicle walls; abundant interfollicular connective tissue.	Compact clusters of spermatogonia lining follicle walls; early spermatogenic activity; presence of phagocytes; abundant connective tissue.
3	Late developing	Enlarged, elongated or oval acini; increasing number of previtellogenic and early vitellogenic oocytes; thinner follicle walls; reduced connective tissue.	Enlarged acini with spermatogonia along periphery and spermatocytes in lumen; initiation of spermiogenesis; reduced connective tissue.
4	Mature (ripe)	Acini fully developed and densely packed with polygonal vitellogenic oocytes; follicle walls indistinct; connective tissue minimal or absent; occasional atresia observed.	Large acini filled with mature spermatozoa; well-developed spermatogenic layers; lumen densely packed with spermatozoa; connective tissue absent.
5	Partially spawned	Evidence of gamete release; partially empty follicles; residual postvitellogenic oocytes; irregular acinar structure; reappearance of connective tissue.	Partially emptied acini; lumen containing residual spermatozoa; presence of phagocytes; early degeneration of germinal tissue; connective tissue reappearing.
6	Spawned / Spent	Collapsed, irregular acini with few or no remaining oocytes; extensive connective tissue; phagocytic activity prominent; signs of resorption.	Reduced follicle size with large empty spaces; few residual spermatocytes; increased connective tissue; active phagocytosis and degeneration of gametes.

In females, progression from the inactive to mature stage was characterized by enlargement of ovarian follicles, a reduction in interfollicular connective tissue and the progressive accumulation of previtellogenic and vitellogenic oocytes (Fig. 2).

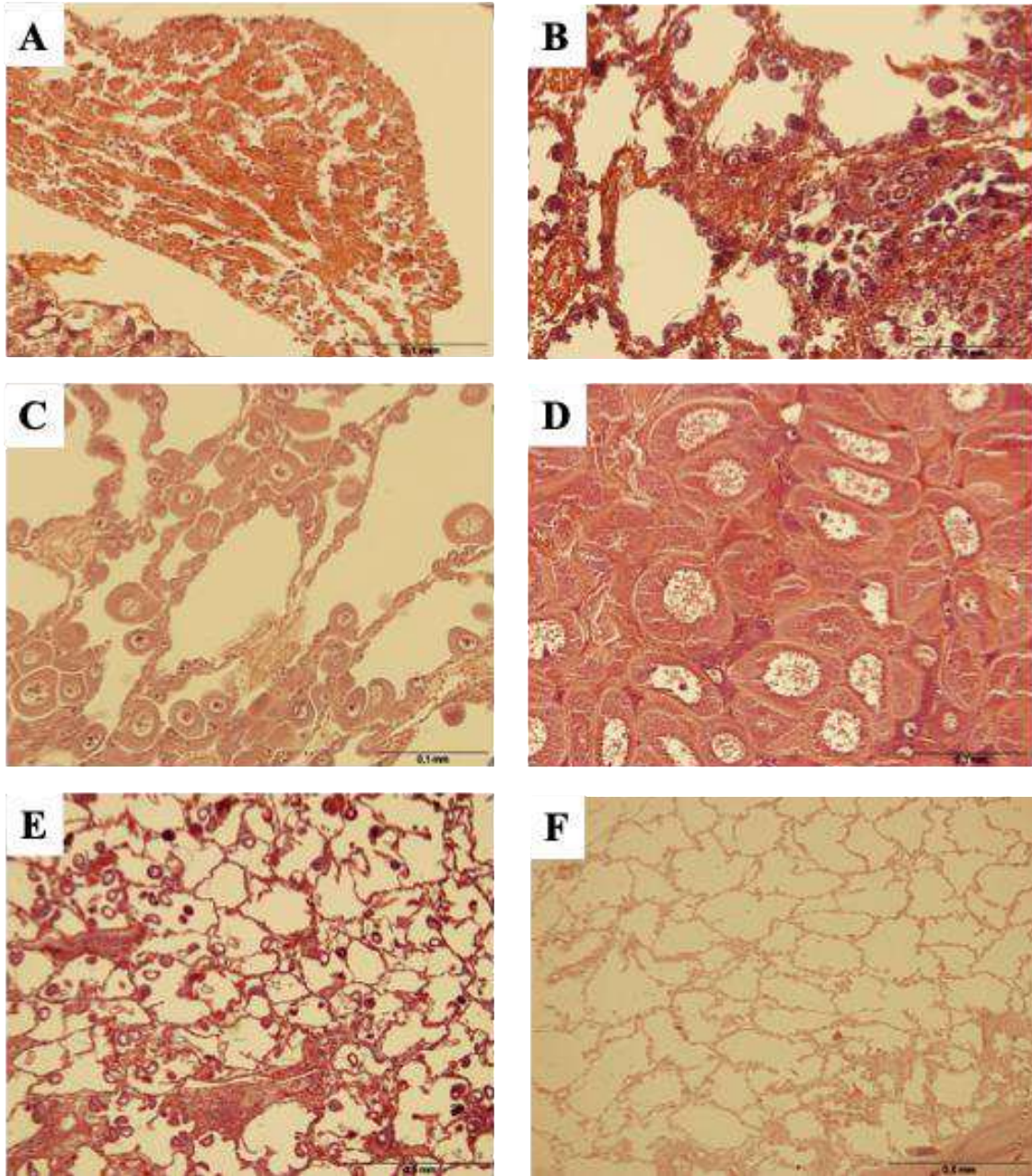


Figure 2. Representative histological stages of female gonadal development in *Mimachlamys varia*: (A) inactive, with abundant connective tissue and poorly developed follicles; (B) early developing, with oogonia and early previtellogenic oocytes along follicular walls; (C) late developing, with enlarged acini containing previtellogenic and vitellogenic oocytes; (D) mature, with acini densely packed with polygonal vitellogenic oocytes; (E) partially spawned, with partly emptied follicles and residual oocytes; and (F)

spent, with collapsed follicles, increased connective tissue and phagocytic activity. H&E staining, scale bar 0.1 and 0.5 mm.

Mature ovaries contained densely packed polygonal vitellogenic oocytes and little remaining connective tissue. In males, maturation was characterized by expansion of the testicular acini, progressive organisation of spermatogenic cell layers and accumulation of spermatozoa within the acinar lumina (Fig. 3). Mature testes contained large acini densely filled with spermatozoa and minimal interacinar connective tissue. Partially spawned and spent gonads in both sexes contained partly emptied or collapsed follicles, residual gametes, increasing amounts of connective tissue and evidence of phagocytic activity.

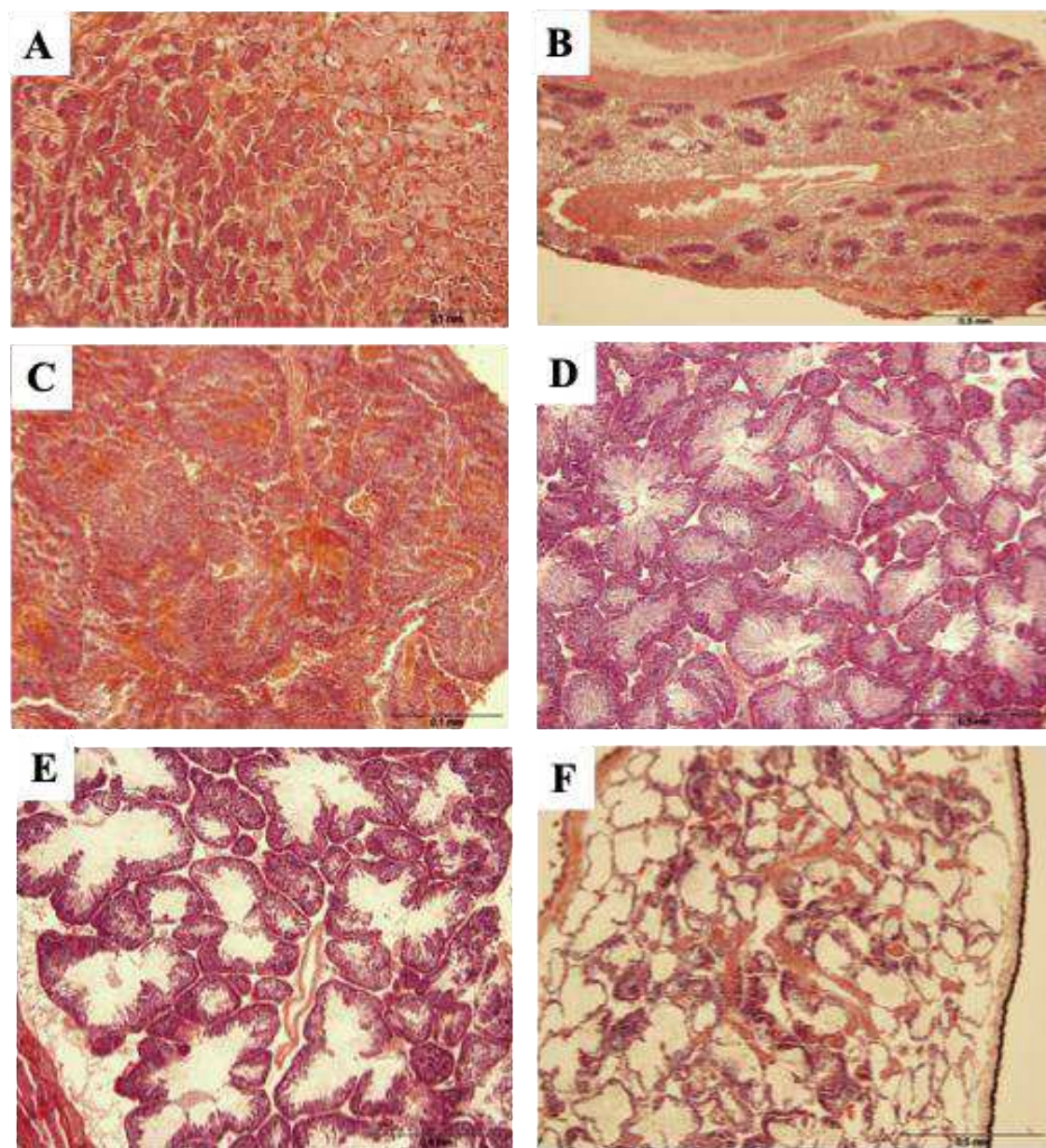


Figure 3. Representative histological stages of male gonadal development in *Mimachlamys varia*: (A) inactive, with poorly differentiated follicles and abundant connective tissue; (B) early developing, with spermatogonia lining follicular walls; (C) late developing, with enlarged acini containing spermatocytes and early spermatids; (D) mature, with lumina densely packed with spermatozoa; (E) partially spawned, with partly emptied acini and residual spermatozoa; and (F) spent, with degenerating follicles, increased connective tissue and phagocytic activity. H&E staining, scale bar 0.1 and 0.5 mm.

Both female-dominant and male-dominant hermaphroditic gonads were observed (Fig. 10). Female-dominant hermaphrodites contained extensive ovarian tissue with developing or vitellogenic oocytes, whereas male-dominant hermaphrodites contained predominantly spermatogenic tissue and acini filled with spermatozoa. Hermaphrodites were also recorded among small individuals weighing 1–5 g and exhibiting early gonadal development.

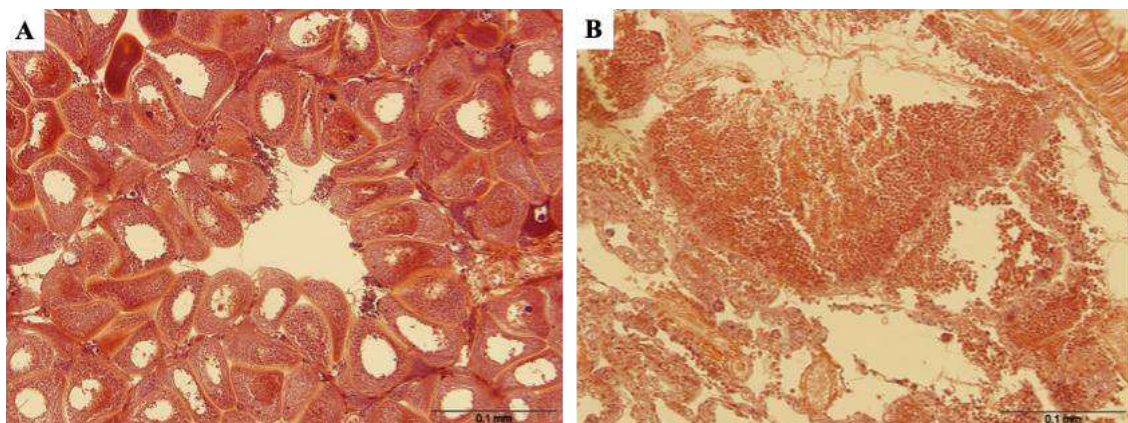


Figure 10. Histological sections of hermaphroditic *Mimachlamys varia*: (A) female-dominant gonad with extensive ovarian tissue and vitellogenic oocytes; and (B) male-dominant gonad with predominant spermatogenic tissue and sperm-filled acini. H&E staining, scale bar 0.1 mm.

Temporal development of female gonads

Female gonadal development showed a distinct seasonal pattern (Fig. 4). During August–October, most females were classified as early or late developing, with growing ovarian follicles containing increasing numbers of previtellogenic and vitellogenic oocytes. The frequency of mature females increased during autumn and winter, and mature ovaries were most prominent during late winter and early spring.

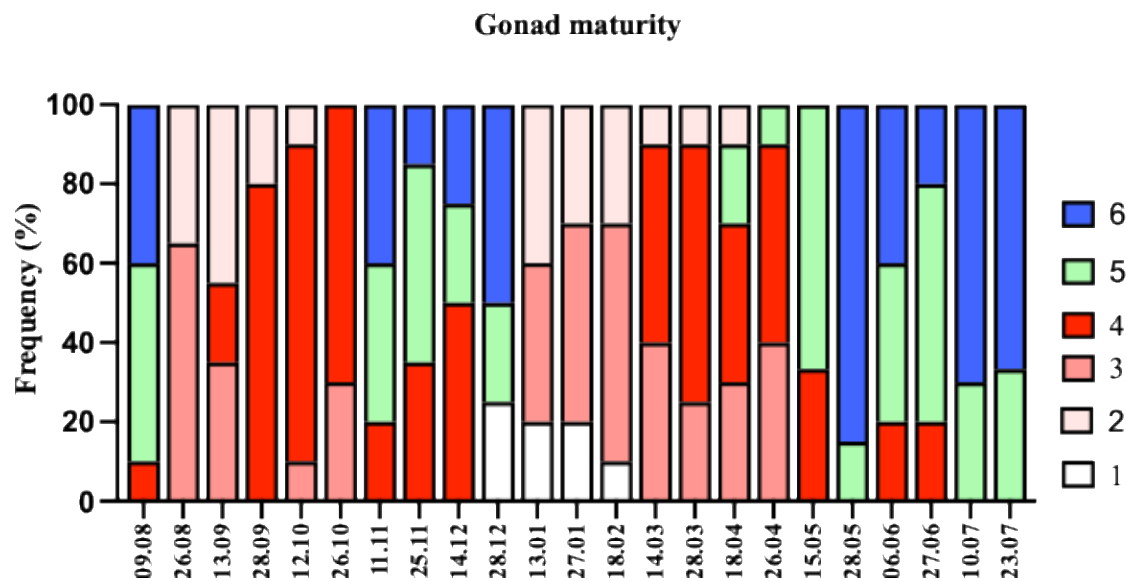


Figure 4. Temporal frequency distribution of female gonadal stages in *Mimachlamys varia* during the annual reproductive cycle in Mali Ston Bay. Stages: 1, inactive; 2, early developing; 3, late developing; 4, mature; 5, partially spawned; and 6, spent.

Partially spawned females first appeared during winter and became increasingly frequent during spring. Partially emptied follicles, residual mature oocytes and reappearing connective tissue were characteristic of this stage. Spent females were recorded mainly from spring to early summer and exhibited collapsed or irregular follicles, few residual oocytes and increased phagocytic activity. Following the principal spawning period, inactive and early developing females became more frequent, indicating the onset of a subsequent cycle of ovarian development.

Temporal development of male gonads

Male gonadal stages showed greater temporal overlap than female stages (Fig. 5). Inactive and early developing males predominated during late summer and early autumn. As autumn progressed, the frequency of late developing testes increased, while inactive stages became less common.

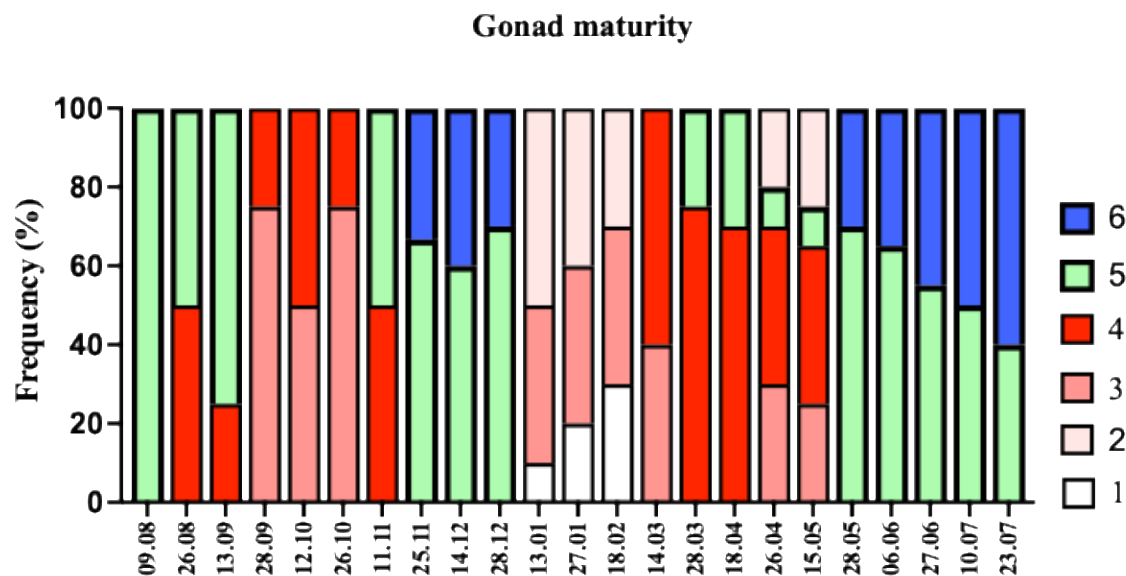


Figure 5. Temporal frequency distribution of male gonadal stages in *Mimachlamys varia* during the annual reproductive cycle in Mali Ston Bay. Stages: 1, inactive; 2, early developing; 3, late developing; 4, mature; 5, partially spawned; and 6, spent.

Mature males were observed from November onwards and were most frequent during winter and early spring. Partially spawned males appeared during winter and became more common during spring. Spent testes were recorded predominantly during late spring and early summer and were characterized by partly or completely emptied acini, residual spermatozoa and increased connective tissue. Developing, mature and partially spawned males occurred concurrently during several sampling periods, demonstrating prolonged population-level male gametogenic activity.

Environmental conditions

Seawater temperature, salinity and chlorophyll *a* concentration varied over the annual cycle (Fig. 6). Seawater temperature declined from approximately 27 °C in late summer to a winter minimum of approximately 8.5–9.0 °C in February and subsequently increased to approximately 27 °C in July. Salinity was comparatively stable, generally ranging between approximately 34 and 38 psu, although a temporary decrease to approximately 31 psu occurred in February. Chlorophyll *a* concentration ranged from approximately 0.14 to 0.64 mg m⁻³ and showed several local maxima, particularly during autumn and in May.

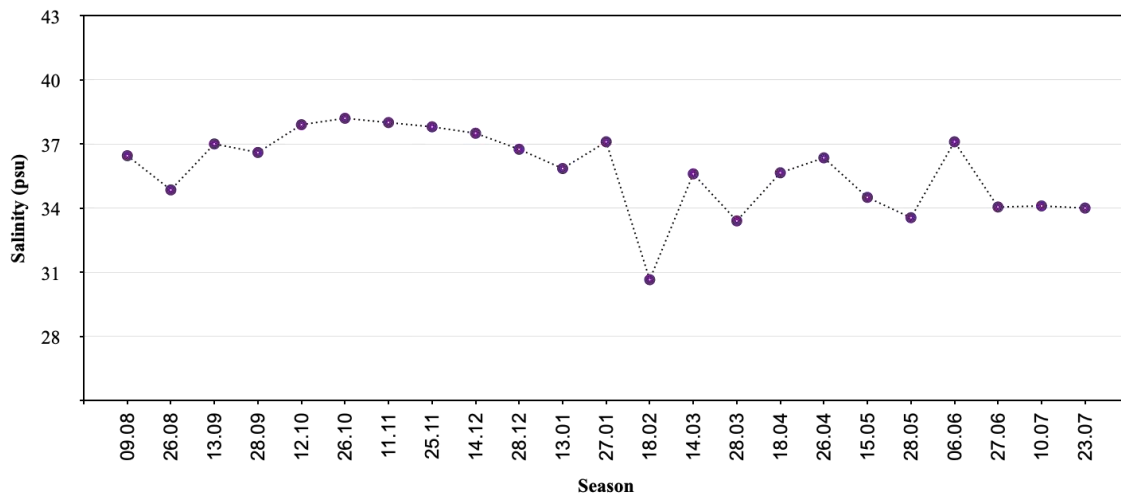
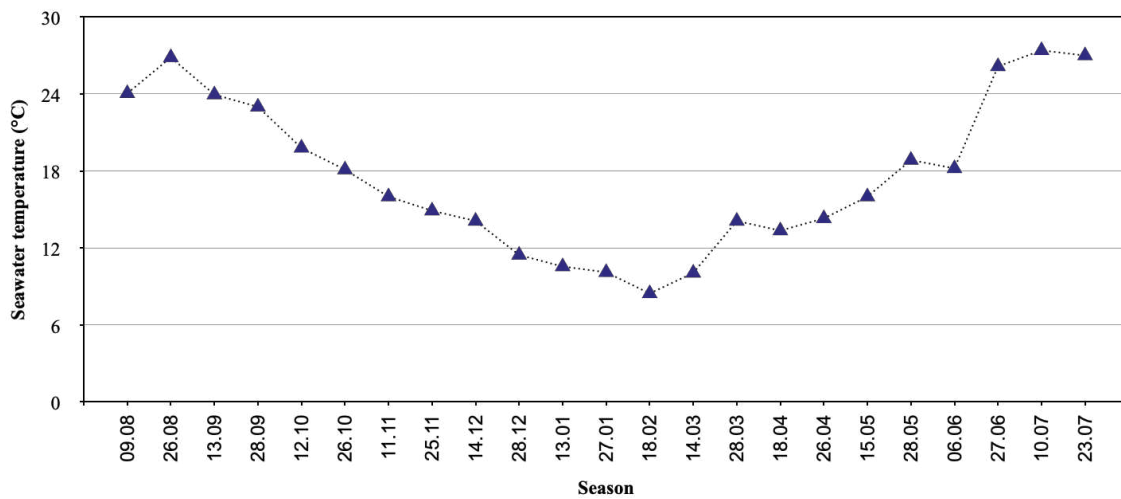
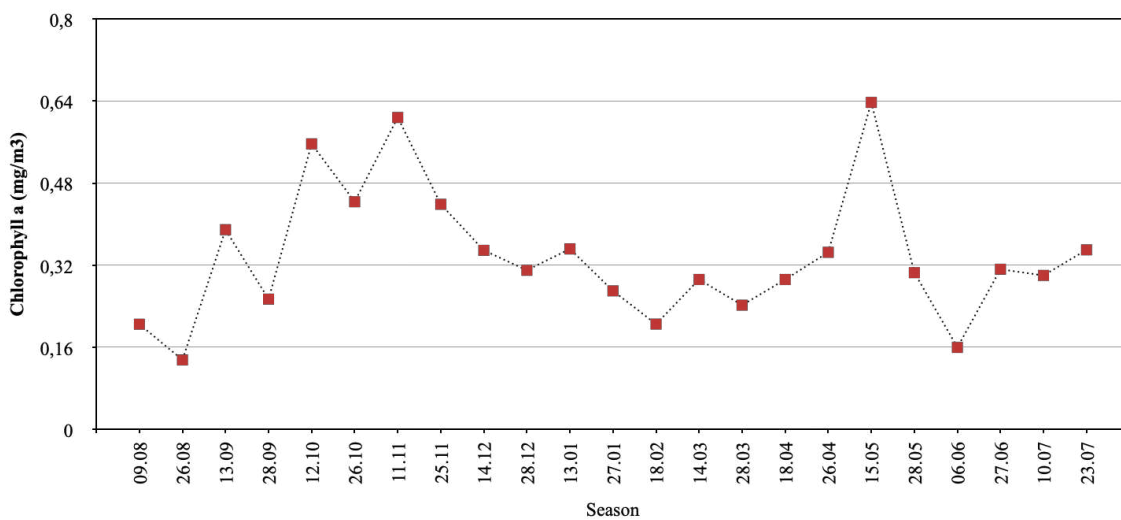


Figure 6. Temporal variation in (A) salinity (psu), (B) seawater temperature (°C) and (C) chlorophyll *a* concentration (mg m⁻³) at the culture site in Mali Ston Bay.

The increasing occurrence of mature gonads overlapped with declining seawater temperatures during autumn and winter. Partially spawned and spent stages became

increasingly frequent from winter through spring and early summer, during the period of minimum and subsequently increasing seawater temperature.

Condition index

Condition index differed significantly among sampling dates (Welch's one-way ANOVA, $F(22, 82.90) = 5.32, p < 0.001$; Fig. 7; Supplementary Table S1). However, CI did not follow a simple monotonic seasonal trajectory. Mean CI ranged from $28.42 \pm 15.34\%$ on 14 March to $47.21 \pm 2.93\%$ on 18 April, while most sampling-date means ranged between approximately 37 and 45%. Games–Howell pairwise comparisons among sampling dates are presented in Supplementary Table S1. No significant correlations were detected between mean CI and seawater temperature, salinity or chlorophyll *a* concentration at the sampling-date level (all $p > 0.05$).

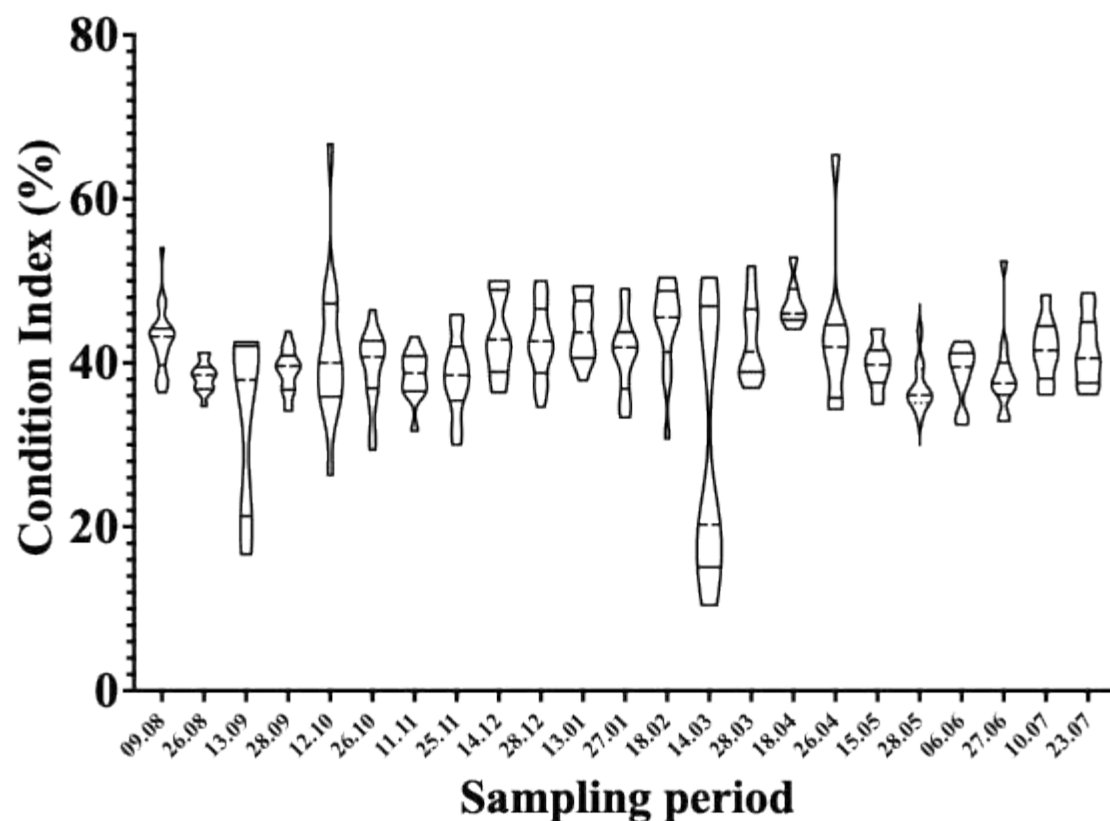


Figure 7. Temporal variation in condition index (CI) of *Mimachlamys varia*. Violin plots show the distribution for each sampling date; central lines and bars indicate the median and interquartile range, respectively.

Gonadosomatic index

Gonadosomatic index differed significantly among sampling dates (Welch's one-way ANOVA, $F(22, 79.54) = 15.73, p < 0.001$; Fig. 8; Supplementary Table S2). Mean GSI generally increased from late summer into autumn, from $5.79 \pm 1.79\%$ on 9 August to $15.29 \pm 5.50\%$ on 12 October. Values fluctuated during November–January before reaching a maximum of $21.37 \pm 8.27\%$ on 18 February. GSI remained comparatively elevated on several dates during March and April, after which it declined markedly. The lowest mean GSI was recorded on 28 May ($2.54 \pm 2.34\%$), and values remained low throughout June and July. This decline coincided temporally with increasing frequencies of partially spawned and spent gonads. Mean GSI was negatively correlated with seawater temperature across sampling dates (Pearson's correlation, $r = -0.670, n = 23, p < 0.001$). No significant relationships were detected between GSI and salinity or chlorophyll a concentration (both $p > 0.05$).

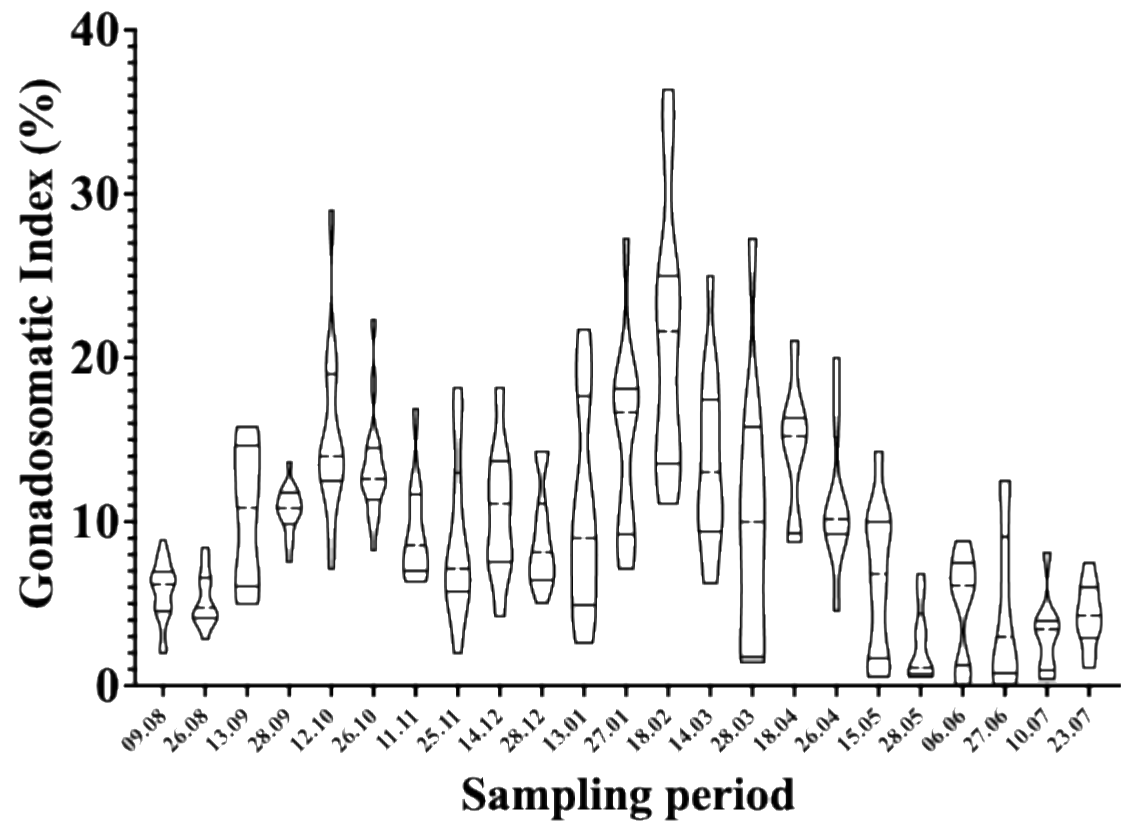


Figure 8. Temporal variation in gonadosomatic index (GSI) of *Mimachlamys varia*. Violin plots show the distribution for each sampling date; central lines and bars indicate the median and interquartile range, respectively.

Oocyte perimeter

Oocyte-perimeter measurements are presented descriptively because multiple oocytes were measured within individual females and female identifiers were not retained in the archived dataset (Fig. 9; Supplementary Table S3). Mean oocyte perimeter varied from 0.10 ± 0.01 mm on 23 July to 0.20 ± 0.04 mm on 18 April. Relatively high mean values were also recorded on 25 November and 14 December (both approximately 0.19 mm), whereas lower values were recorded on 14 March and 15 May (both approximately 0.12 mm). The temporal distribution of oocyte perimeter was characterized by alternating higher and lower values rather than by a single progressive increase followed by a uniform post-spawning decline.

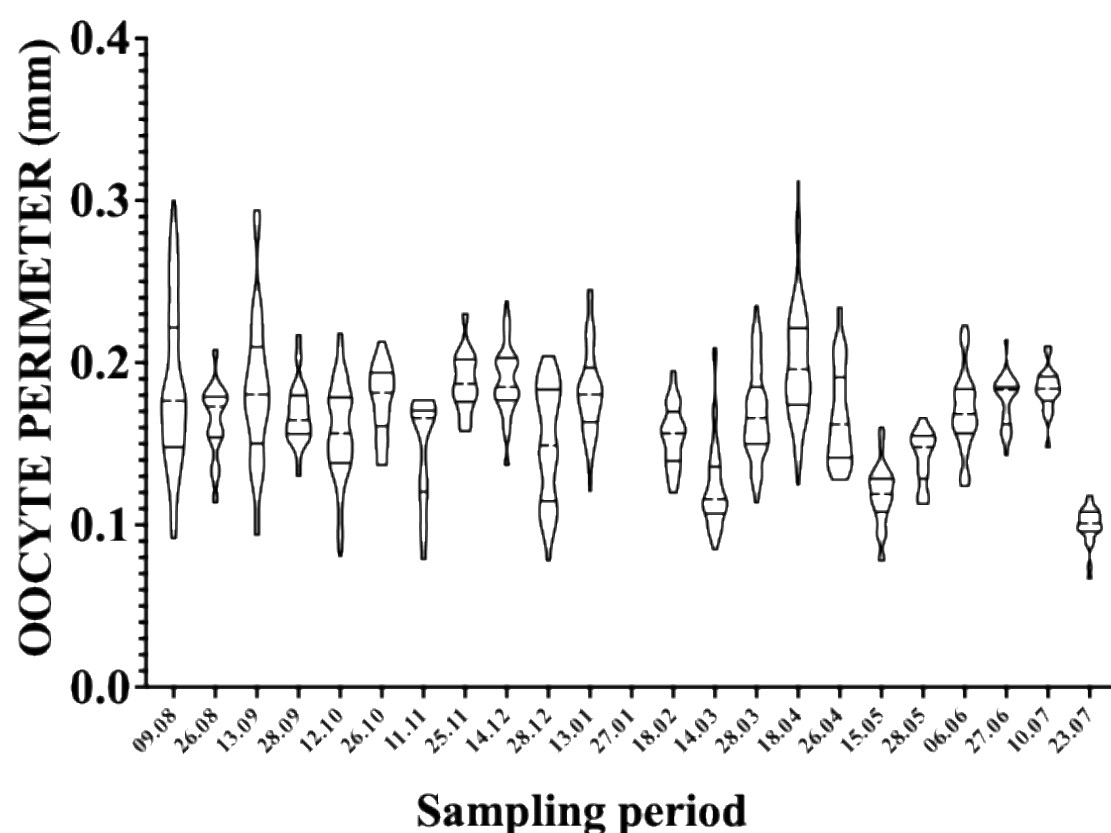


Figure 9. Temporal variation in oocyte perimeter (mm) in female *Mimachlamys varia*. Violin plots show the distribution for each sampling date; central lines and bars indicate the median and interquartile range, respectively.

Discussion

To our knowledge, this study provides the first integrated histological assessment of the reproductive cycle, sex composition and hermaphroditism of *Mimachlamys varia* in the

eastern Adriatic Sea. Gonadal histology, gonadosomatic index (GSI), condition index (CI), oocyte morphometry and environmental monitoring collectively indicated a prolonged and asynchronous reproductive cycle. Male gametogenic activity extended across much of the year, whereas female maturation was concentrated during autumn and winter, followed by an increasing occurrence of partially spawned and spent stages from winter to early summer. GSI increased during gonadal development and declined markedly during the main period of gamete release. The substantial temporal overlap among developing, mature, partially spawned and spent gonads is therefore consistent with repeated partial spawning rather than a single synchronized reproductive event.

The pattern observed in Mali Ston Bay is compatible with the reproductive plasticity previously reported for Atlantic *M. varia*, although its timing and duration differed among locations. In the Bay of Brest, partial spawning was followed by renewed gonadal development and subsequent gamete release (Shafee and Lucas 1980), while spawning and settlement varied among years on the west coast of Ireland (Burnell 1991). In Galicia, depth-related differences in temperature and food conditions were associated with reproductive development and reserve-storage cycles (Iglesias et al. 2012). Extended or variable reproductive activity also occurs in other pectinids and Adriatic bivalves (Cantillán et al. 2005; Mladineo et al. 2007; Crnčević et al. 2013), but species exposed to similar environmental regimes can follow markedly different reproductive and energy-allocation strategies (Ezgeta-Balić et al. 2022). The productive and seasonally variable conditions of Mali Ston Bay may therefore support several reproductive strategies rather than imposing a single spawning schedule. Thus, the prolonged and comparatively unsynchronized cycle recorded here appears biologically plausible for *M. varia*, while differences in sampling design, culture conditions, histological classification and study year limit direct comparisons among populations.

Temporal spreading of gamete release could increase the probability that at least some larvae encounter favourable conditions for feeding, dispersal and settlement and may therefore act as a form of temporal risk spreading. However, this adaptive interpretation cannot be demonstrated from gonadal histology alone because larval abundance, survival, dispersal and recruitment were not measured. A prolonged population-level spawning period may also result from variation among individuals in size, physiological condition, reproductive history or local food exposure rather than from a coordinated bet-hedging

strategy. The results therefore demonstrate temporal reproductive heterogeneity, but its consequences for recruitment remain to be tested directly.

Male and female reproductive development differed clearly. Mature males appeared earlier and remained present for a greater portion of the annual cycle, whereas female maturation was more concentrated and was followed by a clearer increase in partially spawned and spent stages. This pattern may partly reflect the greater energetic investment required for the production of yolk-rich oocytes than for spermatozoa, because vitellogenesis depends on the acquisition or mobilisation of proteins, lipids and essential fatty acids (Barber and Blake 2016). Males may consequently maintain reproductive readiness under a broader range of physiological conditions, while female maturation may be more strongly constrained by body size and energetic status. Earlier male maturation has also been reported in *Pinna nobilis* cultured in Mali Ston Bay, although that species principally spawns under rising spring and summer temperatures (Kožul et al. 2024), illustrating species-specific responses to a shared environment.

The sex-composition data are consistent with protandric sex expression in *M. varia*. Males and females occurred in broadly similar numbers in the examined sample; hermaphrodites represented 5.2%, and the smallest sexually differentiated individuals were male. This agrees with age-related protandry in Atlantic *M. varia*, in which younger or smaller scallops function predominantly as males and female expression becomes more frequent with increasing age and size (Burnell 1995). It is also consistent with the size-advantage model: increasing body size can substantially increase potential egg production, whereas male reproductive success may be less strongly size-dependent, favouring initial male function followed by female function (Ghiselin 1969).

These observations do not, however, prove protandric sex change. The study was cross-sectional, individual scallops were not followed through a male-to-female transition, and small individuals were selectively added to assess early differentiation. The overall counts therefore describe the examined sample rather than an unbiased population sex ratio; a formal assessment of sex parity would require random sampling within comparable size classes. Female-dominant and male-dominant hermaphroditic gonads may represent different transitional states, but neither the direction nor the permanence of change can be inferred from a single histological observation. Hermaphrodites occurred at several sampling dates rather than being restricted to one narrow period, which is compatible

with asynchronous transition among individuals, but only 13 were identified and statistical power to assess seasonality was limited. Detection may also depend on section number and anatomical position if ovarian and testicular tissues are unevenly distributed within the gonad. Systematic sampling across body-size classes and examination of multiple sections per individual would provide more reliable estimates of hermaphroditism and its relationships with size and season.

Temperature was the environmental variable most clearly associated with reproductive development. Mean GSI was negatively correlated with seawater temperature, histological maturation progressed as temperatures declined during autumn and winter, and GSI reached its maximum near the winter temperature minimum. Partially spawned and spent gonads then became more frequent from winter through spring and early summer. Thus, cooling coincided with gonadal development, while gamete release extended across both low and subsequently increasing temperatures.

This correlation should not be interpreted as evidence that declining temperature directly initiated gametogenesis. Temperature covaried with photoperiod, food conditions and other unmeasured seasonal factors, and a one-year observational study cannot separate their independent effects or establish causality. Bivalve reproduction is generally regulated by interactions among thermal history, food supply, endogenous rhythms and physiological condition rather than by a single environmental variable (Sastry 1979; Gosling 2003; Barber and Blake 2016). Atlantic *M. varia* likewise responds to combinations of temperature, depth and food availability (Iglesias et al. 2012). Pronounced seasonal variation has also been recorded in reproductive and physiological indices of Adriatic *Pecten jacobaeus* (Topić Popović et al. 2021; Šebalj et al. 2026), whereas *Pinna nobilis* in Mali Ston Bay enters its principal spawning period under rising spring and summer temperatures (Kožul et al. 2024). These contrasting responses indicate that temperature acts within a species-specific reproductive framework rather than as a universal spawning trigger for Adriatic bivalves.

The absence of significant relationships between GSI and contemporaneous chlorophyll *a*, or between GSI or CI and salinity, should also be interpreted cautiously. A temporal lag may separate food uptake and reserve accumulation from subsequent investment in gonadal tissue. In addition, chlorophyll *a* is a broad proxy for phytoplankton biomass and does not reflect taxonomic composition, particle size, digestibility, essential fatty-acid

availability or non-phytoplankton particulate matter. Reproductive development may consequently depend more strongly on cumulative food exposure and stored reserves than on chlorophyll *a* measured at the sampling date (Darriba et al. 2005; Joaquim et al. 2011; Barber and Blake 2016). Salinity was comparatively stable apart from a temporary winter decrease and may not have varied sufficiently to reveal a response. The findings therefore indicate no detectable relationships within the temporal resolution and environmental ranges studied, rather than demonstrating that food availability or salinity has no reproductive influence. Higher-resolution food measurements, lagged analyses and experimental exposure to a broader salinity range would be required to test these possibilities.

Among the quantitative indicators, GSI corresponded most closely with histological development. Its autumn-winter increase reflected gonadal growth, while the marked decline from May onward coincided with increasing frequencies of partially spawned and spent gonads. Nevertheless, GSI alone cannot distinguish fully mature tissue from partially evacuated follicles or residual gametes. Its agreement with histology supports its usefulness for seasonal monitoring, but histological validation remains necessary for accurate staging.

Oocyte perimeter alternated between higher and lower values rather than showing a single progressive increase followed by a uniform post-spawning decline. This heterogeneity is compatible with overlapping cohorts of developing and mature oocytes, partial gamete release and renewed oogenesis during an extended reproductive period. Similar persistence of developed oocytes has been reported in *Pecten maximus* (Duinker and Nylund 2002). However, because several oocytes were measured within each female and female identity was not retained, the measurements were not independent biological replicates and were appropriately interpreted descriptively. Future analyses should retain individual identity and use female-level summaries or mixed-effects models with oocytes nested within females.

CI varied among sampling dates but did not show the progressive decline expected if somatic reserves were continuously transferred to the gonad. The lowest mean occurred in mid-March, followed by a rapid recovery and the maximum value in April. This irregular trajectory may reflect reproductive expenditure, short-term feeding conditions, tissue hydration, body-size composition or other physiological processes, and the March

decrease cannot be attributed specifically to reserve mobilisation. Because CI was calculated from wet tissue and total body mass, it is an indirect and potentially variable measure of energetic condition. Studies in *M. varia* and other bivalves show that gametogenesis may be supported by different combinations of recently assimilated food and stored glycogen, proteins and lipids (Darriba et al. 2005; Mladineo et al. 2007; Joaquim et al. 2011; Iglesias et al. 2012). Direct measurements of glycogen, proteins, total lipids and fatty-acid composition would therefore be needed to determine how reserve use contributed to the present reproductive cycle.

The reproductive schedule has practical implications for broodstock management. Advanced gonadal development was most frequent from late autumn through early spring, identifying this period as the most promising window for collecting mature or near-mature broodstock. The prolonged cycle may broaden the collection window, but population-level asynchrony and partial spawning may make it difficult to obtain synchronized batches. Histological or validated non-lethal assessment of individual reproductive status could therefore improve broodstock selection before conditioning or spawning induction. Such information is increasingly used to guide hatchery planning in scallop aquaculture (Uriarte et al. 2001; Budiyati et al. 2025). However, egg quality, fertilization, larval development and spat production were not evaluated so the present results cannot establish that autumn-winter collection will maximize hatchery performance. Controlled conditioning experiments are required to test how collection stage, temperature and diet affect spawning synchrony, gamete quality and larval survival.

The findings should be interpreted within the defined scope of the study. Sampling at a single culture site over one annual cycle provided a detailed seasonal description of reproduction under consistent suspended-culture conditions, although reproductive timing may vary among years, locations, depths, culture systems and natural populations. The inclusion of smaller individuals enabled assessment of early sexual differentiation, while the observed sex proportions should be regarded as descriptive of the sampled material rather than as population-level estimates. Environmental observations focused on temperature, salinity and chlorophyll *a* and therefore did not capture the potential contribution of factors such as food quality, particulate organic matter, hydrodynamics and photoperiod. These considerations do not alter the principal evidence for a prolonged

and asynchronous reproductive cycle but indicate that multi-year and multi-site studies would be valuable for evaluating the broader generality of the observed patterns.

Conclusion

This study provides an integrated histological description of the annual reproductive cycle of *Mimachlamys varia* under suspended culture in the eastern Adriatic Sea. Gonadal development was prolonged and asynchronous, with maturation occurring predominantly during autumn and winter and partially spawned and spent stages becoming more frequent from winter to early summer. GSI reflected this temporal pattern and was negatively associated with seawater temperature, whereas CI showed a less consistent seasonal trajectory. The smallest sexually differentiated specimens were male, and low-frequency hermaphrodites occurred at multiple sampling dates, a pattern consistent with, but not definitive evidence of, protandric sex change. These findings identify late autumn to early spring as a promising period for obtaining broodstock with advanced gonadal development. Controlled conditioning and spawning experiments are now required to determine whether this reproductive window improves gamete quality, larval performance and hatchery reliability.

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Statements and Declarations

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Competing interests

The authors have no relevant financial or non-financial interests to disclose.

Author contributions

Mara Rathman, Jakša Bolotin and Nenad Antolović contributed to field sampling and maintenance of the experimental scallops. Histological processing and evaluation were performed by Josip Barišić, Ivančica Strunjak-Perović, Natalija Topić Popović and Rozelindra Čož-Rakovac. Data analysis and interpretation were performed by Mara Rathman and Josip Barišić. Mara Rathman and Josip Barišić prepared the first draft of the manuscript. All authors reviewed and approved the final manuscript.

Data availability

The datasets generated and analysed during the current study are available from the corresponding author on reasonable request.

Ethics approval

No approval of a research ethics committee was required because the experimental work was conducted with an unregulated invertebrate species.

Supplementary

Sampling date	CI Mean $\pm$ SD (%)	Statistical group
09.08	42.74 $\pm$ 4.03	abd
26.08	38.31 $\pm$ 1.85	ce
13.09	33.31 $\pm$ 10.99	abcde
28.09	39.03 $\pm$ 2.67	bce
12.10	41.57 $\pm$ 9.79	abcde
26.10	39.33 $\pm$ 4.70	bcde
11.11	38.48 $\pm$ 3.07	bce
25.11	38.49 $\pm$ 4.96	bcde
14.12	43.27 $\pm$ 5.01	abcde
28.12	42.55 $\pm$ 4.61	abcde
13.01	44.11 $\pm$ 3.80	ad
27.01	41.08 $\pm$ 4.78	abcde
18.02	44.53 $\pm$ 5.49	abcd
14.03	28.42 $\pm$ 15.34	bcde
28.03	42.83 $\pm$ 4.98	abcde
18.04	47.21 $\pm$ 2.93	a
26.04	43.34 $\pm$ 9.75	abcde
15.05	39.71 $\pm$ 2.81	bcde
28.05	37.05 $\pm$ 2.93	e
06.06	38.56 $\pm$ 3.48	bcde
27.06	38.69 $\pm$ 5.26	bcde
10.07	41.67 $\pm$ 3.94	abcde
23.07	41.54 $\pm$ 4.21	abcde

S1. Condition index (CI) of *Mimachlamys varia* by sampling date. Values are mean $\pm$ SD. Different superscript letters indicate pairwise differences according to Welch's ANOVA and Games–Howell pairwise comparisons ($p < 0.05$).

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Sampling date	GSI Mean $\pm$ SD (%)	Statistical group
09.08	5.79 $\pm$ 1.79	cdefh
26.08	5.27 $\pm$ 1.66	defh
13.09	10.46 $\pm$ 4.44	abcdefgh
28.09	10.70 $\pm$ 1.50	abg
12.10	15.29 $\pm$ 5.50	ab
26.10	13.31 $\pm$ 3.34	ab
11.11	9.40 $\pm$ 3.20	bcdg
25.11	8.82 $\pm$ 5.14	abcdefgh
14.12	10.62 $\pm$ 4.21	abcdfg
28.12	9.04 $\pm$ 3.12	bcdg
13.01	10.79 $\pm$ 6.41	abcdefg
27.01	15.01 $\pm$ 5.95	ab
18.02	21.37 $\pm$ 8.27	a
14.03	13.67 $\pm$ 5.40	ab
28.03	10.02 $\pm$ 7.89	abcdefgh
18.04	14.45 $\pm$ 4.26	abc
26.04	11.37 $\pm$ 4.79	abcdefg
15.05	6.56 $\pm$ 4.42	cdefh
28.05	2.54 $\pm$ 2.34	h
06.06	5.05 $\pm$ 3.17	defh
27.06	4.61 $\pm$ 4.73	defgh
10.07	3.21 $\pm$ 2.44	eh
23.07	4.31 $\pm$ 1.97	efh

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718 S2. Gonadosomatic index (GSI) of *Mimachlamys varia* by sampling date. Values are
719 mean $\pm$ SD. Different superscript letters indicate pairwise differences according to
720 Welch's ANOVA and Games–Howell pairwise comparisons ($p < 0.05$).

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Sampling date	Oocyte perimeter Mean $\pm$ SD (mm)
09.08	0.18 $\pm$ 0.05
26.08	0.16 $\pm$ 0.02
13.09	0.18 $\pm$ 0.05
28.09	0.17 $\pm$ 0.02
12.10	0.16 $\pm$ 0.03
26.10	0.18 $\pm$ 0.02
11.11	0.15 $\pm$ 0.03
25.11	0.19 $\pm$ 0.02
14.12	0.19 $\pm$ 0.02
28.12	0.15 $\pm$ 0.04
13.01	0.18 $\pm$ 0.03
18.02	0.16 $\pm$ 0.02
14.03	0.12 $\pm$ 0.03
28.03	0.17 $\pm$ 0.03
18.04	0.20 $\pm$ 0.04
26.04	0.17 $\pm$ 0.03
15.05	0.12 $\pm$ 0.02
28.05	0.14 $\pm$ 0.02
06.06	0.17 $\pm$ 0.02
27.06	0.18 $\pm$ 0.02
10.07	0.18 $\pm$ 0.01
23.07	0.10 $\pm$ 0.01

S3. Oocyte perimeter (mm) in female *Mimachlamys varia* by sampling date. Values are mean $\pm$ SD.

738 Highlights

- 739 • First integrated histological characterization of reproduction in *Mimachlamys*
740 *varia* from the eastern Adriatic Sea.
- 741 • Gonadal development was prolonged and asynchronous, with histological
742 patterns consistent with repeated partial spawning.
- 743 • GSI was negatively associated with seawater temperature, but not with salinity or
744 contemporaneous chlorophyll *a*.
- 745 • The smallest sexually differentiated scallops were male, while low-frequency
746 hermaphrodites occurred at multiple sampling dates.
- 747 • The reproductive schedule identifies seasonal windows relevant to broodstock
748 collection and hatchery conditioning.

Supplementary Files

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