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Reproductive dynamics of the sympatric topshells *Phorcus lineatus* and *Phorcus sauciatus* (Gastropoda: Trochidae) on a rocky intertidal coast in southern Portugal

Paula Moura[1], Paulo Vasconcelos[1], Fábio Pereira[1],
André N. Carvalho[1], Miguel B. Gaspar[1,2]

[1]Instituto Português do Mar e da Atmosfera (IPMA, I.P.), Avenida 5 de Outubro s/n, 8700-305 Olhão, Portugal.
(PM) (Corresponding author) E-mail: pmoura@ipma.pt. ORCID iD: https://orcid.org/0000-0003-3411-9918
(PV) E-mail: paulo.vasconcelos@ipma.pt. ORCID iD: https://orcid.org/0000-0002-2119-2297
(FP) E-mail: fpereira@ipma.pt. ORCID iD: https://orcid.org/0000-0002-1806-0189
(ANC) E-mail: andre.carvalho@ipma.pt. ORCID iD: https://orcid.org/0000-0002-6517-7013
(MBG) E-mail: mbgaspar@ipma.pt. ORCID iD: https://orcid.org/0000-0001-9245-8518
[2]Centro de Ciências do Mar (CCMAR), Universidade do Algarve, Campus de Gambelas, 8005-139 Faro, Portugal.

Summary: The present study aimed to describe the reproductive cycle of the topshells *Phorcus lineatus* and *Phorcus sauciatus* from an intertidal rocky shore in the Algarve, southern Portugal. Based on two years of monthly sampling performed between January 2017 and December 2018, the study involved analyses of gonad histology and estimation of the mean gonadal index, aiming to investigate their relationship with environmental variables. Both topshell species are dioecious and showed synchrony in the reproductive dynamics between sexes. Indeed, the reproductive cycle of *P. lineatus* and *P. sauciatus* exhibited similar patterns, with scarcity of inactive gonads and prolonged periods with mature and spawning individuals. The gonadal index closely reflected the species' reproductive cycle, which is apparently influenced by seasonal fluctuations in air and seawater temperatures. Additionally, some atmospheric and oceanographic conditions, such as daylight duration and wave height, were also correlated with gonad ripening and spawning of *P. lineatus*, and wind speed with gonad ripening and spawning of *P. sauciatus*. Overall, the present study provided valuable information to propose harvesting management measures aiming to ensure the sustainable exploitation of this shellfish resource, namely a closed season in the harvesting of both topshell species in September–October, covering their spawning peak in southern Portugal.

Keywords: trochid gastropods, intertidal rocky shore, gametogenesis, spawning season, mean gonadal index, shellfish harvesting, management measures, Atlantic Ocean.

Dinámica reproductiva de los burgados simpátricos *Phorcus lineatus* y *Phorcus sauciatus* (Gastropoda: Trochidae) en una costa intermareal rocosa en el sur de Portugal

Resumen: El presente estudio tuvo como objetivo describir el ciclo reproductivo de los burgados simpátricos *Phorcus lineatus* y *Phorcus sauciatus* de una costa intermareal rocosa en el Algarve (sur de Portugal). Basado en un muestreo mensual de 2 años realizado entre enero de 2017 y diciembre de 2018, el estudio implicó análisis de la histología de las gónadas y estimación del índice gonadal medio (IG), con el objetivo de investigar su relación con variables ambientales. Ambas especies de burgados son dioicas y presentaron sincronía en la dinámica reproductiva entre sexos. De hecho, el ciclo reproductivo de *P. lineatus* y *P. sauciatus* exhibió patrones similares, con escasez de gónadas inactivas y períodos prolongados con individuos maduros y en desove. El IG refleja fielmente el ciclo reproductivo de la especie, que aparentemente está influenciado por las fluctuaciones estacionales de las temperaturas del aire y del agua de mar. Además, algunas condiciones atmosféricas y oceanográficas particulares, como la duración de la luz del día y la altura de las olas, también se correlacionaron con la maduración gonadal y el desove de *P. lineatus*, y la velocidad del viento con la maduración gonadal y el desove de *P. sauciatus*. En general, el presente estudio proporcionó información valiosa para proponer medidas de gestión del marisqueo destinadas a garantizar la explotación sostenible de estos recursos marisqueros, a saber, una temporada de veda en el marisqueo de ambas especies de burgados durante septiembre y octubre, cubriendo su pico de desove en el sur de Portugal.

Palabras clave: gasterópodos troquídeos, costa rocosa intermareal, gametogénesis, temporada de desove, índice gonadal medio, marisqueo, medidas de gestión, océano Atlántico.

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INTRODUCTION

The topshells *Phorcus lineatus* (da Costa, 1778) and *Phorcus sauciatus* (F.C.L. Koch, 1845) are herbivorous marine snails (Gastropoda: Vetigastropoda) belonging to the family Trochidae. These species are commonly found in shallow and sheltered shores and play important roles in intertidal food webs (Hickman and McLean 1990, Herbert 1992, Sousa et al. 2018), controlling algal growth, shaping intertidal communities and recycling nutrients (Knox 2000, Crothers 2001).

The species *P. lineatus* occurs in the upper half of the intertidal zone (Desai 1966), reaching its northern distribution limits in Wales and Ireland (Kendall 1987, Donald et al. 2012). Its distribution is continuous along the Portuguese, Spanish and French Atlantic coasts, and its southern limit is reached on the Atlantic coast of Morocco (Mieszkowska 2005). However, even within these areas its distribution is patchy and erratic (Fretter and Graham 1977). The species *P. sauciatus* is a common subtropical topshell with a northern limit in the Iberian Peninsula (Galicia) and the same southern limit as *P. lineatus*, and also occurs in the archipelagos of Madeira, Canary and more recently also in the Azores (Rubal et al. 2014, Costa 2015, Baptista et al. 2021).

These topshell species are commonly found on intertidal rocky shores along the coast of mainland Portugal (Macedo et al. 1999, Donald et al. 2012, Cabral 2020). Both species inhabit an extreme and dynamic coastal environment, which exposes them to thermal and hydric stresses (Raffaelli and Hawkins 1999, Ramírez et al. 2005).

Classical descriptions of the reproductive biology of diverse trochid species distributed elsewhere were reported by Williams (1965), Duch (1969), Underwood (1972, 1974a) and Grange (1976). However, the general knowledge on the biology and ecology of *P. lineatus* and *P. sauciatus*, especially on their reproductive cycle, is extremely scarce. The distribution and shell morphometrics of both species were analysed along the Portuguese coast by Costa (2015) and Vasconcelos et al. (2022). The zonation of *P. sauciatus* in Tenerife, Canary Islands, was studied by Alfonso et al. (2015), and its biological invasion in the Azores archipelago was reported by Ávila et al. (2015) and Baptista et al. (2021). Finally, the reproductive dynamics of *P. lineatus* in Asturias, Spain, was described by Bode et al. (1986).

Topshells are harvested for human consumption in some coastal communities. For instance, commercial and recreational harvesting of *P. sauciatus* are ancestral and traditional activities in the Madeira (Sousa et al. 2020), Azores (Ávila et al. 2015, Sousa et al. 2020) and Canary archipelagos (Ramírez et al. 2005, Tuya et al. 2006, Alfonso et al. 2015), whereas in mainland Portugal topshells are mainly collected recreationally and consumed locally and sporadically (Vasconcelos et al. 2022). In Portugal, the regulations currently in force for harvesting topshells (sensu lato) stipulate a minimum conservation reference size (MCRS=12 mm in shell height, D.R. 2011) for both commercial and recreational catches (D.R. 2014) of *P. lineatus* and *P. sauciatus*, in order to ensure the collection of mostly adult and mature individuals from exploited populations. In addition, information on the species' reproductive cycle is also crucial to promote the sustainable management of commercially and recreationally exploited topshell populations (Underwood 1979, Perry et al. 1999, Boman et al. 2018).

The present study aimed to describe the gametogenic cycle of *P. lineatus* and *P. sauciatus* from southern Portugal, as well as to evaluate the influence of biologically/ecologically relevant atmospheric and oceanographic parameters on the reproductive dynamics of these sympatric intertidal species. Overall, this study delivers valuable baseline information for the proposal of management measures (namely seasonal closures for both professional and recreational harvesting activities), which might contribute to promote the long-term sustainable exploitation of these topshell species.

MATERIALS AND METHODS

Study area and field sampling

Topshells of both *P. lineatus* and *P. sauciatus* were caught manually during low tide in Praia da Luz (37°05.1'N, 08°43.8'W), a rocky shore in the municipality of Lagos (Algarve coast, southern Portugal)

(Fig. 1). Approximately 20 specimens of each species were collected monthly during two consecutive years (January 2017–December 2018). In the laboratory, specimens were separated by species, counted, measured for shell height (SH) using a digital calliper (precision=0.01 mm) and weighed for total weight on a top-loading digital balance (precision=0.01 g).

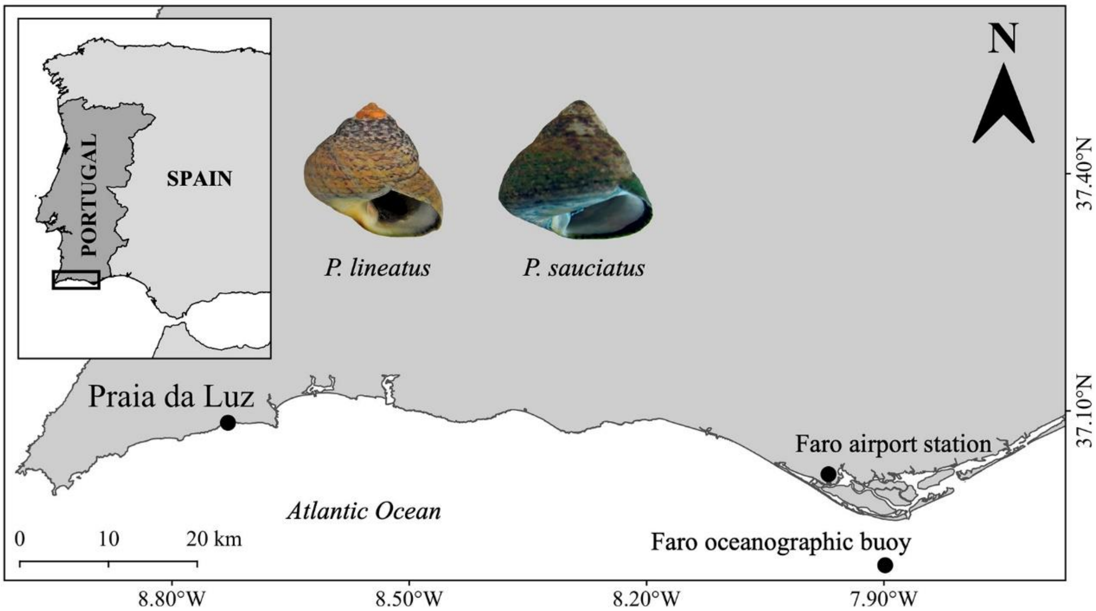

Fig. 1. – Map showing the location of the collecting site (black box) for the topshells *Phorcus lineatus* and *Phorcus sauciatus* on intertidal rocky shores at Praia da Luz in Lagos (Algarve coast, southern Portugal).

In order to analyse their possible influence on the species reproductive dynamics, data on surface seawater temperature (SST) and significant wave height (WH) recorded during the study period at the Faro oceanographic buoy (closest buoy to the collecting site: 36°54.3'N, 07°53.9'W) of the Portuguese Hydrographic Institute (I.H. 2020) was collected. In addition, data on air temperature (AT), daylight duration (DD) and wind speed (WS) recorded in the same period at the Faro airport station (37°01.2'N, 07°58.2'W) were acquired from Weather Underground (2024).

Gonad histology and mean gonadal index

Specimens of *P. lineatus* and *P. sauciatus* were fixed in Davidson solution for 48 hours and then the preserved tissues were dehydrated, infiltrated and embedded in paraffin wax. The visceral coils (digestive gland and gonad) were cut (7 µm thick) using an automated rotary microtome and stained with haematoxylin and eosin.

Sex and gonad maturity stages were assigned after examining the histological sections under an optical microscope (magnifications of 40×, 100× and 200×). Gonad maturity stages were identified and classified using the microscopic maturation scale previously employed by Vasconcelos et al. (2008, 2012) for the banded murex (*Hexaplex trunculus*) and the purple dye murex (*Bolinus brandaris*): resting (stage I), pre-active (stage II), active (stage III), ripe (stage IV), partially spent (stage V) and spent (stage VI). Whenever diverse developmental stages were observed within a single gonad, the classification criterion was based on the prevailing maturity stage identified in that gonad.

Subsequently, a numerical ranking was assigned to each maturity stage (resting=0; pre-active=2; active=3; ripe=4; partially spent=5; spent=1) in order to estimate the mean gonadal index (GI) following the equation proposed by Seed (1976):

$$GI = \frac{\sum \text{inds. each stage} \times \text{stage ranking}}{\text{total inds. each month}}$$

Statistical analyses

The sex ratio in monthly samples of *P. lineatus* and *P. sauciatus*, expressed as the proportion of males per female (F:M), was compared with parity (1:1) using the chi-square test (χ^2-test).

A correlation matrix between the monthly frequency of males and females at each gonad maturity stage was performed to analyse the synchronization of the reproductive cycle between sexes in both topshell species. Another correlation matrix was produced to analyse the possible relationships between the mean GI of both topshell species and atmospheric and oceanographic parameters in the region during the study period (AT, SST, DD, WS and WH). Data normality was previously checked using the Shapiro-Wilk test and then the correlation between variables was assessed through Pearson (r) or Spearman (ρ) coefficients when data were normally or non-normally distributed, respectively.

Data treatment and statistical procedures were performed using the software packages Microsoft Excel (2016) and R statistical language (R Core Team 2024), with statistical significance level considered for $P<0.05$.

RESULTS

Sex ratio

A total of 455 individuals of *P. lineatus* (17.2±2.4 mm SH) were examined, comprising 52.7% males (17.2±2.4 mm SH), 44.8% females (17.4±2.4 mm SH) and 2.4% sexually undifferentiated individuals (14.9±2.2 mm SH). Overall, the 472 specimens of *P. sauciatus* (15.6±2.3 mm SH) analysed included 51.9% males (15.6±2.2 mm SH), 46.8% females (15.8±2.3 mm SH) and 1.3% sexually undifferentiated individuals (12.0±1.8 mm SH). During the study period, the sex ratio of both topshell species was not significantly different from parity (1F:1M) (*P. lineatus*, χ^2=2.919, P=0.086; *P. sauciatus*, χ^2=2.634, P=0.105). Regarding the monthly samples, only *P. lineatus* in May 2018 showed an unbalanced and male-biased sex ratio (1F:3.8M, χ^2=6.368, P=0.011), as did *P. sauciatus* in three months of 2017, January (1F:2.7M, χ^2=4.545, P=0.033), February (1F:2.8M, χ^2=4.263, P=0.039) and March (1F:2.8M, χ^2=4.263, P=0.039).

Gonad histology and reproductive cycle

Photomicrographs of histological sections of *P. lineatus* and *P. sauciatus*, showing the various gonad maturity stages and the most relevant features of gametogenesis, are illustrated in Figures 2 and 3, respectively. Both topshell species are dioecious (i.e. have separate sexes) and their reproductive cycles exhibited similar patterns, with general synchronization between sexes (Figs. 4 and 5). For both species, the Spearman (ρ) correlations established between the monthly frequency of males and females at each gonad maturity stage during the two-year study period confirmed the synchronism in the reproductive cycle between sexes (Table 1). The monthly frequencies of *P. lineatus* and *P. sauciatus* at each stage of gonad maturity are presented in Figures 6 and 7, respectively. Both species displayed residual occurrence of inactive gonads (stage I – resting) and extended periods with prevailing mature (stage IV – ripe) and spawning individuals (stage V – partially spent).

In general, *P. lineatus* displayed a very short resting period in 2017, which was virtually absent in 2018 (as evidenced by the scarcity of inactive and less developed gonads). Specimens at earlier developmental stages (II and III) were found between January and April 2017, and those stages were much rarer in 2018, with only a few ripe individuals (III) occurring mostly between March and June. Except in early 2017, *P. lineatus* showed ripe and spawning gonads (IV and V) almost throughout the entire study period (Fig. 6).

Similarly, inactive gonads of *P. sauciatus* were quite scarce and only observed in a few months spread through 2017. Pre-active and active individuals (stages II and III) were mostly recorded from January to April 2017 and between February and May 2018. The topshell *P. sauciatus* also exhibited a continuous presence of spawning gonads during long periods, nearly all individuals being assigned to stages IV (ripe) and V (partially spent) between May 2017 and January 2018 and from June to December 2018 (Fig. 7).

Atmospheric and oceanographic parameters *vs* mean gonadal index

The months with lowest and highest mean values of atmospheric and oceanographic parameters recorded in 2017 and 2018 are summarized in Table 2. The mean GI of both topshell species displayed positive correlations with air and seawater temperatures, namely *P. lineatus* (AT, ρ=0.638, P<0.01; SST, ρ=0.597, P<0.01) and *P. sauciatus* (AT, ρ=0.483, P<0.05; SST, ρ=0.680, P<0.01). The mean GI of *P. lineatus* showed a positive correlation with daylight duration (DD, ρ=0.421, P<0.05). By contrast, the topshells' mean GIs appeared to be negatively influenced by other atmospheric and oceanographic parameters, namely WS and WH. Indeed, negative correlations were obtained between *P. lineatus* GI and WH (ρ=−0.584, P<0.01) and between *P. sauciatus* GI and WS (ρ=−0.523, P<0.01) (Table 3).

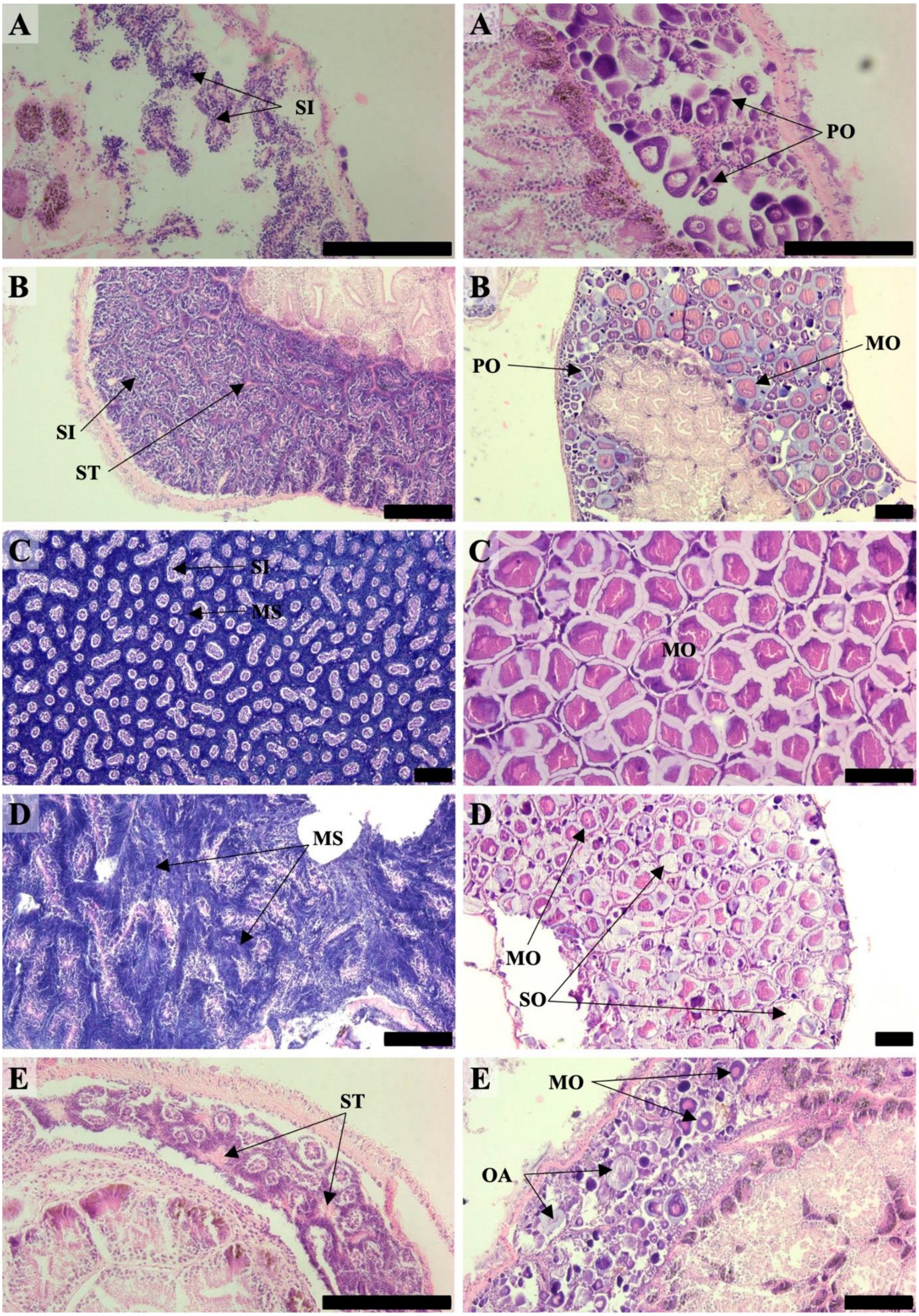

Fig. 2. – Histological sections displaying the gonad maturity stages in males (left) and females (right) of *Phorcus lineatus* from the Algarve coast (southern Portugal): A, pre-active; B, active; C, ripe; D, partially spent; E, spent. Abbreviations: MO, mature oocytes; MS, mature spermatozoa; OA, oocyte atresia; PO, previtellogenic oocytes; SI, spermatids; SO, spawned oocyte; ST, spermatozoa tails. Scale bars: 200 µm.

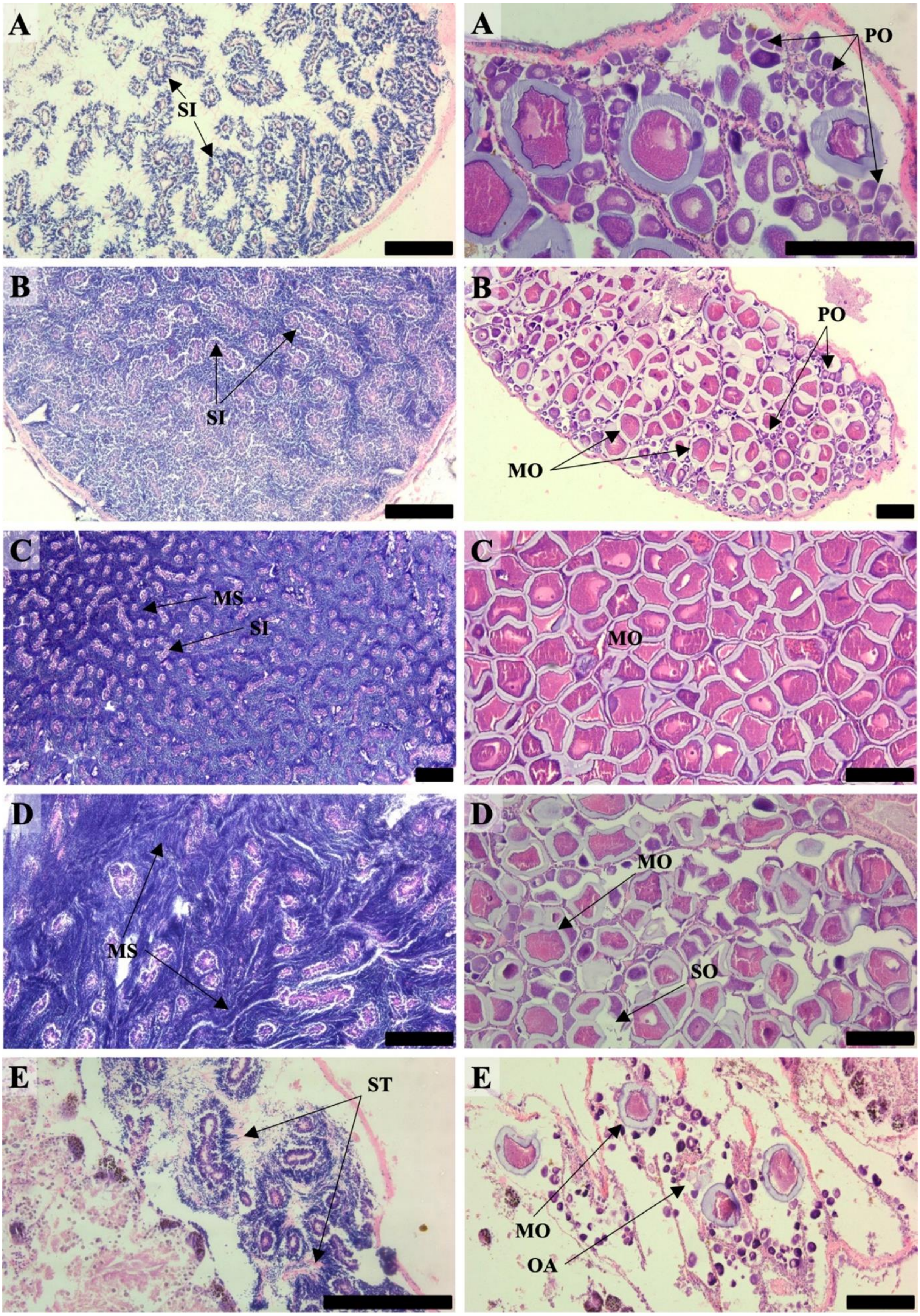

Fig. 3. – Histological sections displaying the gonad maturity stages in males (left) and females (right) of *Phorcus sauciatus* from the Algarve coast (southern Portugal): A, pre-active; B, active; C, ripe; D, partially spent; E, spent. Abbreviations: MO, mature oocytes; MS, mature spermatozoa; OA, oocyte atresia; PO, previtellogenic oocytes; SI, spermatids; SO, spawned oocyte; ST, spermatozoa tails. Scale bars: 200 μm.

The temporal variation in the mean GI of both topshells species and the respective relationships with relevant atmospheric and oceanographic parameters are illustrated in Figure 8. The GI displayed monthly oscillations throughout the study period, closely reflecting the reproductive cycle of both species. In practice, increasing trends in mean GI reflect gradual gonadal maturation and subsequent spawning events. Higher GIs in both species, corresponding to gonadal ripening and spawning, were spread several times over the two-year study period. In 2017, *P. lineatus* showed higher GI in July (4.88), *P. sauciatus* in June (4.85) and both species in September (4.94 and 4.71, respectively), the warmest month in both air (AT=24.7±1.4°C) and seawater temperatures (SST=22.0±1.9°C). In 2018, warmer AT and SST were recorded between August and October, being reflected in relatively high GIs (range: 4.35–5.00) from July to October in *P. lineatus* and from June to December in *P. sauciatus* (Fig. 8).

Table 1. – Spearman (ρ) correlations established between the monthly frequency (%) of *Phorcus lineatus* and *P. sauciatus* males and females at each gonad maturity stage during the two-year study period on the Algarve coast, southern Portugal. (M, males; F, females; gonad maturity stages I, II, III, IV, V and IV).

		Stage I	Stage II	Stage III	Stage IV	Stage V	Stage VI
Phorcus lineatus	(M×F)	ρ=0.988 *P*<0.001	ρ=0.603 *P*=0.002	ρ=0.766 *P*<0.001	ρ=0.754 *P*<0.001	ρ=0.696 *P*<0.001	ρ=0.674 *P*<0.001
Phorcus sauciatus	(M×F)	ρ=0.960 *P*<0.001	ρ=0.662 *P*<0.001	ρ=0.876 *P*<0.001	ρ=0.551 *P*=0.005	ρ=0.790 *P*<0.001	ρ=0.413 *P*=0.045

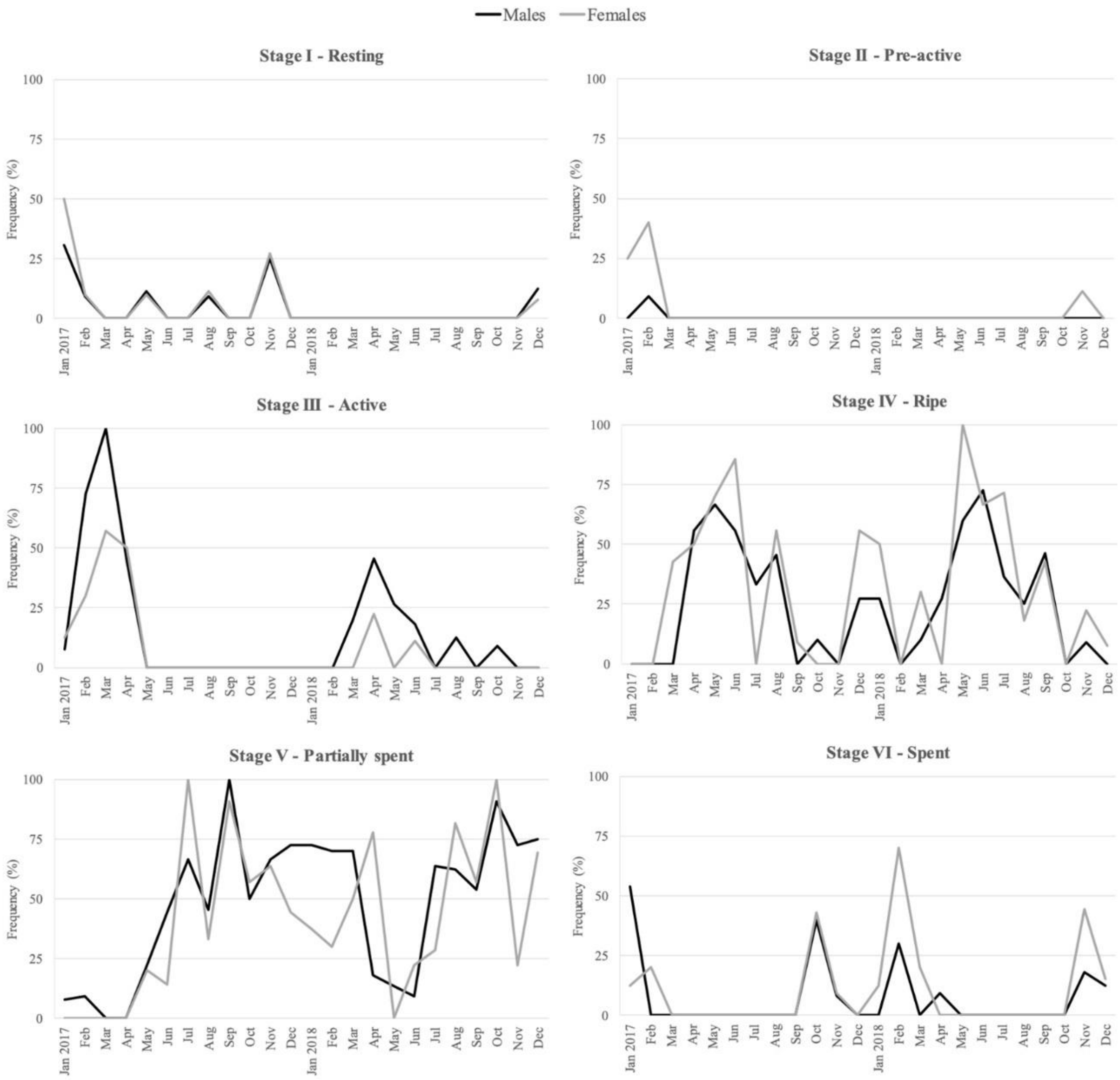

Fig. 4. – Monthly frequency of *Phorcus lineatus* males and females at each gonad maturity stage during the two-year study period on the Algarve coast, southern Portugal.

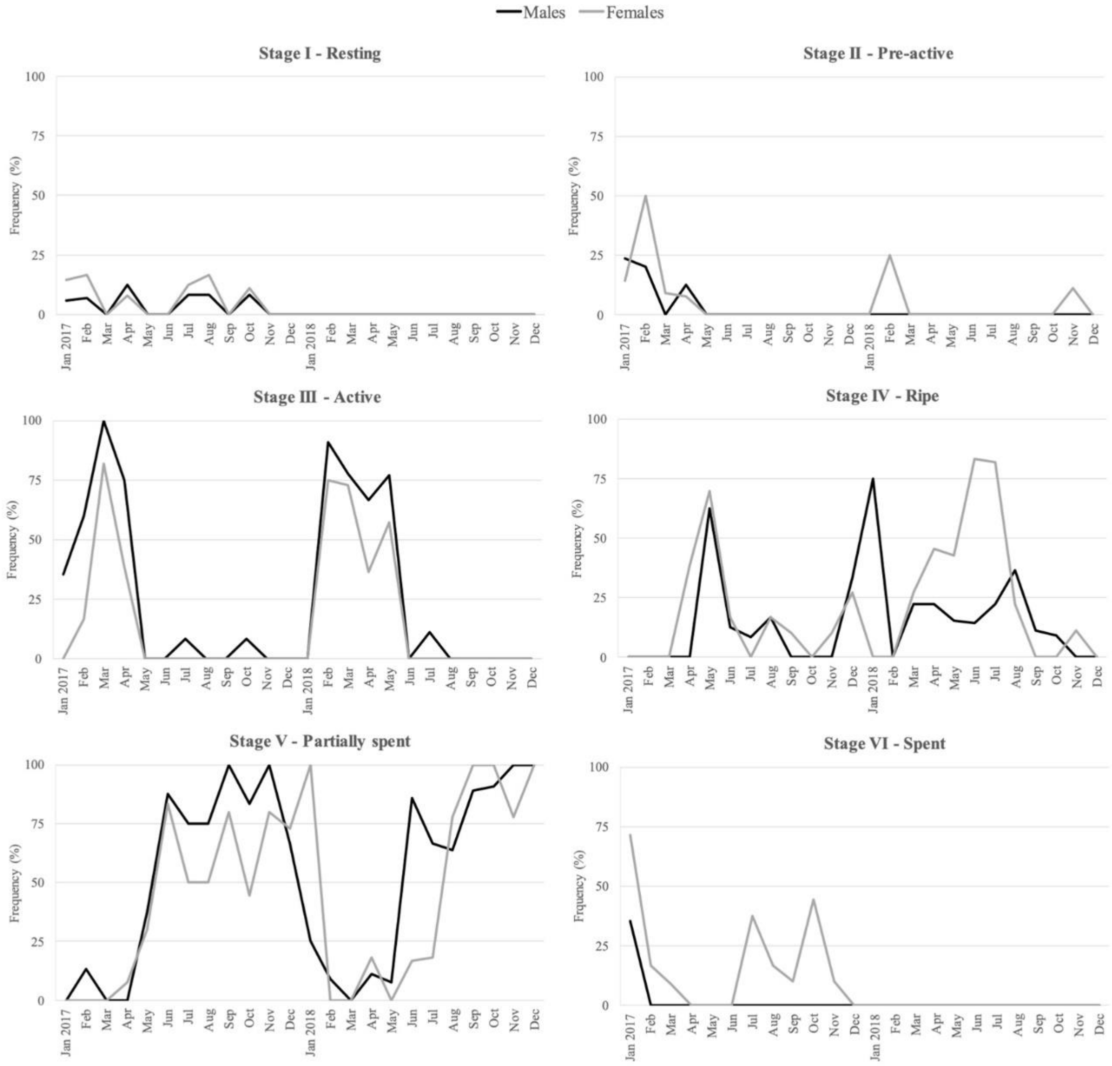

Fig. 5. – Monthly frequency of *Phorcus sauciatus* males and females at each gonad maturity stage during the 2-year study period on the Algarve coast, southern Portugal.

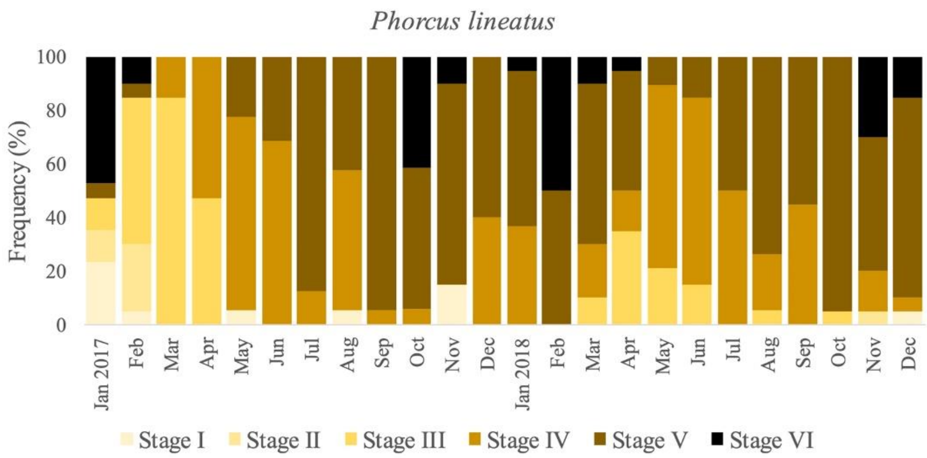

Fig. 6. – Monthly frequency of gonad maturity stages in *Phorcus lineatus* during the two-year study period on the Algarve coast, southern Portugal.

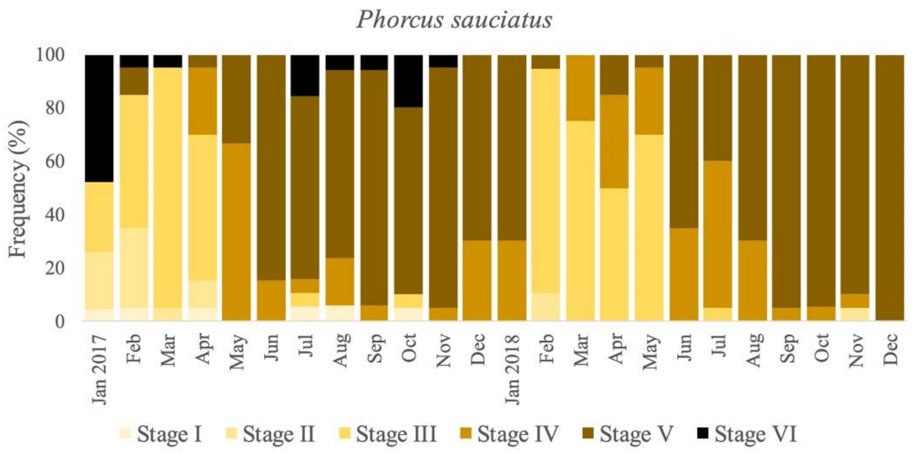

Fig. 7. – Monthly frequency of gonad maturity stages in *Phorcus sauciatus* during the two-year study period on the Algarve coast, southern Portugal.

Table 2. – Lowest and highest monthly mean values of atmospheric and oceanographic parameters recorded during the two-year study period on the Algarve coast, southern Portugal. (AT, air temperature; SST, surface seawater temperature; DD, daylight duration; WS, wind speed; WH, wave significant height).

	2017		2018	
	Minimum	Maximum	Minimum	Maximum
AT (ºC)	Feb 13.2±1.8	Sep 24.7±1.4	Feb 11.8±1.8	Aug 25.7±2.5
SST (ºC)	Feb 15.4±0.4	Sep 22.0±1.9	Mar 14.7±0.4	Oct 23.6±0.8
DD (h)	Jan 9.7	Jul 14.7	Jan 9.8±0.1	Jul 14.7±0.1
WS (km/h)	Oct 12.4±3.8	Feb 17.4±8.0	Sep/Dec 12.4±2.6; 12.4±5.0	Apr 19.8 ±6.5
WH (m)	Aug – Oct 0.7±0.2	Feb 1.4±0.6	Jul/Sep 0.6±0.2	Apr/Dec 1.2±0.4; 1.2±0.5

Table 3. – Spearman (ρ) correlations established between the mean gonadal index (GI) of *Phorcus lineatus* and *P. sauciatus* and diverse atmospheric/oceanographic parameters (AT, air temperature; SST, surface seawater temperature; DD, daylight duration; WS, wind speed; WH, wave significant height) recorded during the two-year study period on the Algarve coast, southern Portugal. Statistically significant correlations (*P*<0.05) are highlighted in bold.

	AT	SST	DD	WS	WH
Phorcus lineatus GI	**ρ=0.638** *P*=0.001	**ρ=0.597** *P*=0.002	**ρ=0.421** *P*=0.041	ρ=−0.283 *P*=0.180	**ρ=−0.584** *P*=0.003
Phorcus sauciatus GI	**ρ=0.483** *P*=0.017	**ρ=0.680** *P*=0.000	ρ=0.097 *P*=0.653	**ρ=−0.523** *P*=0.009	ρ=−0.353 *P*=0.091

DISCUSSION

Like other topshell species, *P. lineatus* and *P. sauciatus* do not exhibit external sexual dimorphism (Desai 1966, Fretter and Graham 1977, Crothers 2001), so their sex is only distinguishable through gonadal examination (Sousa et al. 2018, 2020). These trochid gastropods showed a balanced sexual proportion during almost the entire two-year study period, except in a few months when significantly unbalanced and male-biased sex-ratios were recorded (one month for *P. lineatus* and three months for *P. sauciatus*). Bode et al. (1986) studied the *P. lineatus* population from northern Spain and also recorded a balanced sex ratio (1:1) in the overall sampled individuals. Similarly, no significant deviations from the expected parity sex ratio (1:1) were detected by Lasiak (1987) in three other trochid species (*Monodonta australis*, *Oxystele tabularis* and *O. antoni*) in the Transkei coast (South Africa). Mora et al. (2017) studied the trochid *Cittarium pica* in San Andrés Isla (Gran Caribe) and observed balanced sex-ratios (1:1), except in November when males prevailed over females. In contrast, the overall sex ratio of *P. sauciatus* in Madeira archipelago was female-biased (1:1.3), with females predominating almost year-round, except in February when males were more abundant (Sousa 2019).

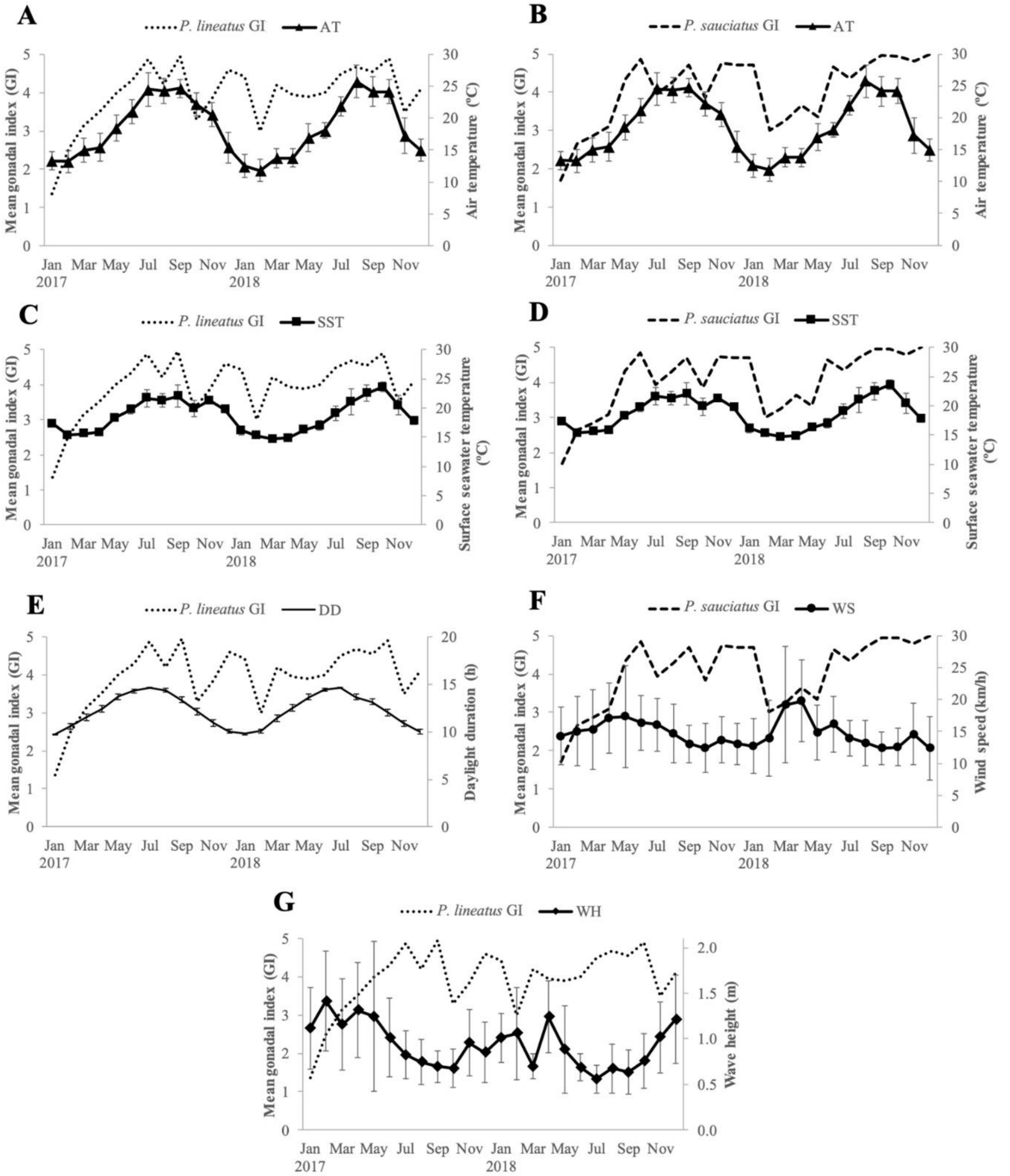

Fig. 8. – Monthly variation in the mean gonadal index (GI) of *Phorcus lineatus* and *P. sauciatus* and its relationship with diverse atmospheric and oceanographic parameters, namely air temperature (AT), surface seawater temperature (SST), daylight duration (DD), wind speed (WS) and significant wave height (WH): A, *P. lineatus* GI vs AT; B, *P. sauciatus* GI vs AT; C, *P. lineatus* GI vs SST; D, *P. sauciatus* GI vs SST; E, *P. lineatus* GI vs DD; F, *P. sauciatus* GI vs WS; G, *P. lineatus* GI vs WH.

In the present study, both topshell species from the Algarve coast displayed synchronous gonadal development between sexes. Several studies have reported synchronized spawning between males and females in marine gastropods worldwide. For instance, *Haliotis asinina* from Heron Reef in Australia (Counihan et al. 2001), *H. trunculus* from Bizerte lagoon in northern Tunisia (Gharsallah et al. 2010) and *Tegula eiseni* (currently accepted as *Agathistoma eiseni*) from Bahía Asunción in Mexico (Vélez-Arellano et al. 2009) exhibited synchronized gametogenic development between sexes. Conversely, in the case of *Tegula euryomphala* collected in La Herradura Bay in Chile and studied under laboratory conditions, males spawned consistently before females (Romero Bastías 2014).

The same trend was also observed in topshell species belonging to the genus *Phorcus*. For instance, *P. lineatus* collected from Aberaeron, mid-Wales, showed a similar pattern of gonadal development between males and females throughout the year (Garwood and Kendall 1985). Moreover, in *P. lineatus* from Asturias, both sexes also behaved similarly during the study period (Bode et al. 1986). Likewise, *P. sauciatus* from Madeira archipelago showed a synchronous gametogenetic cycle between sexes, females and males exhibiting a similar gonadal pattern all year round with only minor dissimilarities in the proportion of mature individuals (Sousa 2019, Sousa et al. 2019).

Both *P. lineatus* and *P. sauciatus* from the Algarve coast showed a clear predominance of mature and spawning gonads throughout the reproductive cycle, which is probably related to successive processes of gonadal re-ripening and partial gametic emissions. This process was more evident in *P. lineatus*, whose individuals exhibited a continuous shift between mature and spawning gonads. Accordingly, both topshells exhibited an extensive spawning season, whereas resting or inactive gonads were only recorded during a short period or were completely absent. In northern Spain, *P. lineatus* also displayed an extensive spawning season (May–November) without a resting period in the reproductive cycle (Bode et al. 1986). Daguzan (1991) analysed *P. lineatus* from the Morbihan coast (France) and observed two reproductive periods per year, one in spring (April–June) and one in autumn (September–October).

By contrast, *P. lineatus* from Plymouth in England (Underwood 1972) and Craig-yr-Wylfa in North Wales (Williams 1965) displayed shorter spawning periods, between June and September and between August and October, respectively, followed by brief resting phases (Fretter and Graham 1977). Indeed, *P. lineatus* populations nearer to northern range limits (North Wales and North Ireland) appear to have a single spawning period, whereas those closer to the centre of the species distributional range have a longer spawning season comprising multiple spawning events (Garwood and Kendall 1985, Bode et al. 1986, Mieszkowska 2005). However, the literature on the reproductive cycle of *P. sauciatus* is extremely scarce, with only one study performed in the Madeira archipelago by Sousa (2019). According to this author, the continuous presence of mature and partially spawned individuals indicates that *P. sauciatus* is reproductively active all year round, with a main spawning season between March and August.

Such differences in topshell reproductive cycles are probably correlated with different environmental parameters. Several authors (e.g. Shanks et al. 2020, Shin et al. 2020, Sukhan et al. 2021) have stated that temperature influences gonad maturation and reproduction in marine gastropods. In general, populations in colder habitats display shorter development phases and more pronounced spawning periods than populations under warmer conditions (Crothers 2001). Furthermore, several studies on the reproductive cycle of Patagonian marine gastropods, namely *Buccinanops cochlidium* (Averbuj et al. 2010), *Odontocymbiola magellanica* (Bigatti et al. 2008), *Tegula patagonica* (currently accepted as *Agathistoma patagonicum*) (Nieto-Vilela et al. 2021) and *Trophon geversianus* (Cumplido et al. 2010), reported that increasing temperature seemed to induce spawning.

Indeed, in the present study the fluctuation of SST revealed inter-annual differences with an atypical pattern recorded in 2017. In fact, during 2017 the SST displayed slight oscillations, exhibiting sequential small increases and decreases between June and November, without reaching very high values (maximum of 22°C in September). In 2018, SST fluctuation showed a distinct pattern, with a gradual increase from March to October (maximum of 23.6°C in October), followed by a pronounced decrease. These dissimilarities in SST between years were reflected in the gametogenic cycles of both species. Individuals in maturity stages I (resting) and II (pre-active) were observed almost only in 2017, and were reflected in some declines in GI during the spring and summer of this year.

Molluscs can be characterized as bradytictic or tachytictic, depending on whether spawning occurs during short or extended periods, with spawning duration being often correlated to latitude, temperature and food availability (Boman et al. 2018, Melchior et al. 2023, Seinor et al. 2023). In addition, species with an extensive geographical distribution might display variable reproductive strategies in both time and intensity of spawning, which have also been related to latitude and its influence on temperature and food availability (Ward and Davis 2002, Freije and Al-Sayed 2009, Ramesh et al. 2010). Therefore, species' reproductive dynamics and duration of spawning are characteristics of each population, linked to biological features and environmental conditions.

Some diversity has been observed in the reproductive cycles and spawning periods of gastropod species. Collin et al. (2017) studied six intertidal gastropod species in the Bay of Panama (*Cerithideopsis californica*, *Crepidula* cf. *marginalis*, *Littoraria variegata*, *Nerita scabricosta*, *Notocochlis chemnitzii* and *Siphonaria maura*) and reported strong differences in the intensity of reproduction and spawning peaks. Some marine gastropods seem to breed continuously throughout the year, while others have well-defined reproductive patterns, with distinct periods of gonad inactivity, gametogenesis and spawning. Indeed, some species release ripe gametes continuously throughout the year (e.g. Aranda et al. 2003, Di Stefano and Giménez 2022), while others display spawning peaks (e.g. Joll 1980, Joska and Branch 1993). Even species inhabiting the same location might exhibit dissimilar reproductive strategies and gametogenic cycles as a specific response to the local environment (Aranda et al. 2003, Collin et al. 2017). Lasiak (1987) reported lacking phylogenetic or geographic relationships in the pattern and timing of reproductive cycles of trochid topshells. Regarding trochoid species, diverse studies reported that *Austrocochlea constricta* (Underwood 1974b), *Cantharidus capillaceus* (Simpson 1977), *Oxystele antoni* and *O. tabularis* (Lasiak 1987) and *Steromphala cineraria* (Underwood 1972) appear to spawn several times throughout the year. Other trochoid species, such as *P. lineatus* and *S. umbilicalis*, have well-defined reproductive cycles with distinct periods of inactivity and spawning (Garwood and Kendall 1985). Moreover, since these topshell species are exposed to severe and instable environmental conditions (Raffaelli and Hawkins 1999, Ramírez et al. 2005), their reproductive cycles are expected to display some spatial and temporal fluctuations (Aranda et al. 2003).

In the present study, the mean GI of *P. lineatus* and *P. sauciatus* showed positive correlations with both air and seawater temperatures, meaning that increases in these environmental parameters prompted gonadal maturation and spawning. The mean GI of *P. lineatus* also displayed positive correlation with daylight duration. Several authors stated that fluctuations in seawater temperature appear to affect gamete development and duration of spawning in gastropod species (e.g. Aranda et al. 2014, Di Stefano and Giménez 2022). In addition, lowest winter temperatures can affect the survival of larvae and juveniles, subsequently impacting recruitment (Kendall et al. 1987). In addition to temperature, the photoperiod also seems to influence gamete release and reproductive activity in marine gastropod species (Himmelman 1999). For instance, the reproductive cycles of various Patagonian gastropods, such as *Adelomelon ancilla* (Penchaszadeh et al. 2009), *B. cochlidium* (Averbujet al. 2010), *O. magellanica* (Bigatti et al. 2008), and *T. geversianus* (Cumplido et al. 2010), appear to be regulated by the quantity of light hours.

Spawning in intertidal organisms appears to be also influenced by other atmospheric and oceanographic conditions, such as, high wind speed, strong wave action and increased phytoplankton (Underwood 1979, Freije and Al-Sayed 2009, Seinor et al. 2023). In particular, trochacean gastropod spawning seems to be also stimulated by intense water movement (Grange 1976). In the present study, a negative correlation was detected between *P. lineatus* GI and WH, indicating that this topshell species spawned preferentially under low-wave conditions. Such spawning behaviour was already expectable, because this species is an indicator of sheltered areas where organisms are more protected from wave action (Costa 2015). However, while calmer sea conditions might be advantageous to avoid larval dispersal after fertilization (Seinor et al. 2023), rough sea conditions might improve population connectivity (Grange 1976) and promote a quick transfer of larvae out of the surf zone, thus avoiding benthic predators (Shanks 1997, Gyory and Pineda 2011).

In addition, *P. sauciatus* GI showed a negative correlation with WS, meaning that spawning occurred preferentially under favourably weaker wind conditions. This species is apparently more tolerant to wave action than *P. lineatus* due to the larger foot and wider shell opening, which are helpful to deal with the risk of displacement by waves (Costa 2015). Furthermore, air temperature fluctuation and desiccation are key stress factors acting on rocky shore organisms (Bertness et al. 2006, Noke 2016). In particular, P. *sauciatus* is highly vulnerable to desiccation due to its large area of contact with the air (Costa 2015, Sousa 2019), which might supress body humidity under strong wind conditions.

In conclusion, both *P. lineatus* and *P. sauciatus* from the Algarve coast exhibited an extensive spawning season, with short resting phase and scarce inactive gonads throughout the year. The reproductive cycle of both species appeared to be influenced by various atmospheric and oceanographic parameters, namely air and seawater temperatures, wind speed and wave height. Overall, the information obtained in this study is relevant for proposing harvesting management measures for the long-term sustainable exploitation of this shellfish resource. Although the commercial harvesting of topshells along the coast of mainland Portugal, including the Algarve coast, can be considered residual (annual reported catches <100 kg in 2008–2014) (DOCAPESCA 2014), both commercial and recreational harvesting activities targeting these species still require suitable tailor-made regulations.

The species *P. lineatus* and *P. sauciatus* co-occurring in the rocky intertidal are relatively difficult to distinguish and are therefore harvested and sold altogether. Based on the extensive spawning period exhibited by both species and on the spawning peaks identified in 2017 and 2018, in order to avoid jeopardizing the harvesters profitability, it would be practical and beneficial to implement a two-month closure in the harvesting activity targeting both topshell species in southern Portugal in September and October. Similarly, in the Madeira archipelago, a closed season for *P. sauciatus* was proposed between February and May

(Sousa 2019), whereas in some locations of Galicia (Spain) topshell harvesting can be banned during two consecutive months depending on specific management measures applied in each shellfish area (D.O.G. 2023). Finally, future studies should also estimate the size at first sexual maturity of both *P. lineatus* and *P. sauciatus* in the Algarve coast in order to confirm the suitability of the minimum conservation reference size for topshells currently in force in Portugal (MCRS=12mm, D.R. 2011), which is less stringent than in Galicia (Spain) (MCRS=15mm, D.O.G. 2012).

DATA AVAILABILITY

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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DECLARATION OF COMPETING INTERESTS

The authors declare no conflict of interests.

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AUTHORSHIP CONTRIBUTION STATEMENT

Paula Moura: Conceptualization, Formal analysis, Investigation, Methodology, Writing – original draft; **Paulo Vasconcelos:** Conceptualization, Investigation, Methodology, Project administration, Writing – review & editing; **Fábio Pereira:** Conceptualization, Formal analysis, Investigation, Methodology, Writing – review & editing; **André N. Carvalho:** Investigation, Methodology, Writing – review & editing; **Miguel B. Gaspar:** Funding acquisition, Project administration, Writing – review & editing.

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