Fisheries Oceanography

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ORIGINAL ARTICLE OPEN ACCESS

Adaptive Reproductive Strategies of Limpets in a Harvest-Influenced Environment

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Received: 1 April 2025 | **Revised:** 1 April 2025 | **Accepted:** 28 May 2025

Funding: This document is the result of a final research project conducted as part of a Bachelor's degree, supported by the Portuguese national funds through the Fundação para a Ciência e a Tecnologia I.P. (FCT), under the project "*Metacommunity dynamics of complex life cycle species in exploited ecosystems*" (LAPACOM), grant number EXPL/MATAPL/0262/2021 and through the strategic project UIDB/04292/2020 and UIDP/04292/2020 awarded to MARE and project LA/P/0069/2020 granted to the Associate Laboratory ARNET. J.V. was supported by the "Grants for the Viera y Clavijo training program for researchers" of the Government of the Canary Islands (VIERA Y CLAVIJO-2022-CIENCIAS-1).

Keywords: Canary Islands | conservation | fecundity | Northeast Atlantic | *Patella aspera* | *Patella crenata*

ABSTRACT

Limpet harvesting is a size-selective activity that primarily removes the largest individuals, leading to reduced reproductive output. This study investigates the fecundity strategies of two limpet species, *Patella aspera* and *Patella crenata*, inhabiting the rocky shores of Gran Canaria. Between September 2023 and April 2024, a total of 288 *P. aspera* and 364 *P. crenata* specimens were sampled from four coastal settlements. Both species exhibited determinate fecundity with synchronous spawning, as evidenced by the progression of dominant oocyte cohorts and the corresponding changes in oocyte size and number throughout the spawning season. Orientation and substrate type significantly influenced fecundity, with the North coast showing a higher number of vitellogenic oocytes, particularly in artificial substrates for *P. crenata*. Natural substrates on the North coast were associated with larger vitellogenic oocytes. Additionally, sex proportions were significantly affected by substrate type, with natural substrates containing a higher proportion of females. In artificial substrates, *P. crenata* exhibited notably higher gonadosomatic index values. The analysis of the gonadosomatic index and oocyte dynamics highlights the adaptive strategies of these limpets to local environmental conditions, contributing to our understanding of reproductive ecology in intertidal habitats. This research not only enhances our understanding of reproductive dynamics in limpets under varying environmental conditions but also emphasizes the importance of habitat and seasonal factors in shaping fecundity strategies. Such studies are crucial for conservation efforts, as they provide essential insights into how environmental pressures and human activities, like harvesting, impact the reproductive success and sustainability of these commercial species.

1 | Introduction

Limpets are essential herbivores in rocky intertidal habitats and hold significant commercial value, but their populations are declining due to habitat alterations and unregulated harvesting (Aguilera et al. 1994; Underwood 2000; Navarro et al. 2005; Ramírez et al. 2008; Burgos-Rubio et al. 2015; Espinosa et al. 2021; Sempere-Valverde et al. 2024). Among these alterations, artificial structures such as seawalls and breakwaters, commonly associated with coastal development, can alter species diversity and reproductive potential by creating low-quality habitats (Hall 2017; Moschella et al. 2005; Airoldi and Bulleri 2011; Sousa et al. 2019; Sedano et al. 2020; Branch et al. 2023; Earp et al. 2023).

Understanding how these environments affect reproductive strategies (e.g., spawning, fecundity, and size at first maturity) is essential for effective coastal management. Recent research has found that certain intertidal species, including limpets, can thrive on artificial coastal structures located in high-energy open sea areas, such as breakwaters and piers, where human access is restricted (García-Gómez et al. 2015; Shabtay et al. 2018). These settings allow these structures to act as small-scale biodiversity reservoirs. For example, breakwaters in the Strait of Gibraltar and Alboran Sea harbors support the densest populations of the endangered limpet *Patella ferruginea* (Gmelin, 1791) (García-Gómez et al. 2011; Ostalé-Valriberas et al. 2022). In addition to the challenges posed by coastal habitat alterations, unregulated harvesting aggravates the decline in limpet populations. Excessive fishing has severely impacted limpet populations worldwide, resulting in smaller specimens, reduced population sizes, skewed female-to-male ratios, and a substantial decline in biomass and reproductive/recruitment output (Branch 1975; Branch and Odendaal 2003; Espinosa et al. 2006, 2009; Guerra-García et al. 2004; Sousa et al. 2019, 2020). To address these impacts, previous research has primarily focused on harvest control measures such as catch and bag limits, gear restrictions, closed seasons, and minimum size limits (Gwinn et al. 2015; Liu et al. 2016; Worm et al. 2009). Studies on fecundity in Patellid limpets are limited and mostly pertain to species like *Patella vulgata* (Ballantine 1961), *Patella ferruginea* (Espinosa et al. 2006; Guallart et al. 2020), and *Patella ordinaria* (Vasconcelos, Ferro, et al. 2023; Vasconcelos, Sousa, et al. 2023). Notably, only two recent studies have examined the fecundity of *Patella aspera* from the Madeira archipelago (Castejón et al. 2022; Vasconcelos, Sousa, et al. 2023).

The Macaronesia region, particularly the Webbnesia ecoregion (Madeira, Selvagens, and Canary Islands), is characterized by unique biodiversity and high endemism, which supports local economies and ecological resilience (Pacheco and Hernandez-Guerra 1999; Ávila 2000; Menezes et al. 2009; Wirtz et al. 2013; Cordeiro and Ávila 2015; Freitas et al. 2019), with limpets, particularly *P. aspera* and *P. ordinaria*, playing a key role in local cultural heritage and generating economic revenue (Hawkins et al. 1999; Moro and Herrera 2000; Ferraz et al. 2001; Turrero et al. 2014). However, this intensified exploitation, particularly post-1980s, has raised substantial concerns about overfishing, including significant furtive capture that undermines conservation efforts (Riera et al. 2016; Sousa et al. 2019). To address these challenges, stringent regulatory and sustainable management measures have been instituted to protect these valuable marine resources and their ecosystems (Martins et al. 2017; Sousa et al. 2020).

In the Canary Islands two species cohabit: *P. aspera* Röding, 1798 and *Patella crenata* Gmelin, 1791 (previously known in the Canaries as *Phos candei crenata* Gmelin, 1791 sensu A. d'Orbigny, 1840; see Faria et al. 2017). The harvesting of commercial limpet species is banned during the closed season from November 1 to April 30 to coincide with their reproductive period. Outside of this season, limpets can be collected with a minimum size established for each species and a daily limit of 3 kg per person, except in protected areas (BOC 2011). Despite these measures, intense exploitation continues to cause significant declines in species such as *P. crenata* and has led to local extinctions of *Patella candei* (previously *P. candei candei)*, which is now restricted to Fuerteventura Island (Côrte-Real et al. 1996; González-Lorenzo et al. 2015; Navarro et al. 2005; Núñez et al. 2003; Weber and Hawkins 2002). One critical aspect often overlooked in current management practices is fecundity, a crucial life history trait influencing reproductive success and population sustainability. Integrating fecundity data could significantly enhance conservation assessments and management strategies (Coleman et al. 2006; Guilhaumon et al. 2015; Vasconcelos, Ferro, et al. 2023; Vasconcelos, Sousa, et al. 2023).

Our team was the first to pioneer the use of fecundity, an often-overlooked life-history trait, in the management of commercial mollusks as part of the LAPACOM Project (2021), which aimed to address significant gaps such as the lack of fecundity data for Patellid limpets—an important group of intertidal mollusks. This research provides the first-ever insights into the fecundity of limpet species in the Canary Islands, offering a crucial framework for implementing new management strategies for limpets with global commercial interest. Building on this foundation, the current study aims to investigate the fecundity strategies of *P. aspera* and *P. crenata* and their integration into coastal management practices in the Canary Islands. The specific objectives are (i) to examine the gametogenic stages of female at a microscopic level, (ii) to explore the criteria used to determine fecundity types in both species, (iii) to compare the number and size of vitellogenic oocytes (VO) between northern and eastern populations of Gran Canaria, and (iv) to compare these parameters between artificial and natural substrates. The primary hypothesis is that fecundity rates will vary significantly between different environmental conditions and substrate types, reflecting the adaptability and resilience of these species to varying ecological contexts.

2 | Materials and Methods

2.1 | Study Area

The Canary Islands are located in the northeastern part of the Central Atlantic (27°37′ to 29°25′N, 13°20′ to 18°10′W), approximately 1000 km from the Iberian Peninsula and about 100 km from the African coast (Carracedo et al. 2013) (Figure 1). The archipelago is influenced by the Canary Current, primarily fed by an eastward branch of the Azores Current, with minor input from the Portugal Current (Mason and Oliveira 2006).

Surfaces temperatures of the Canary Current range between 18°C and 23°C, with salinity from 36 to 37 psu (Hernández-León et al. 2002). Upwelling events in the southeastern Canary Islands transport nutrient-rich, cold waters to the surface, promoting phytoplankton blooms, particularly during the annual chlorophyll peak (Barton et al. 1998; Valdés and Déniz 2015). Throughout the year, chlorophyll concentration is higher near the surface during blooms, while at other times, it appears around the nutricline (Hernández-León et al. 2002).

2.2 | Data Sampling

Between September 2023 and April of 2024, a total of 288 specimens of *P. aspera* (40.1 ± 4.81 mm total shell length, SL) and 364 individuals of *P. crenata* (44.3 ± 5.84 mm SL) were randomly collected from four locations on Gran Canaria: two on the North coast (El Puertillo and El Altillo), and two on the East coast (San Cristóbal and Puerto Taliarte) (Figure 1). Collection sites were selected based on permissible zones for shellfish harvesting (BOC 2011). The northern sites were more exposed to wave action compared to the more sheltered eastern sites. Additionally, limpets were collected from both natural substrates such as platforms and rocks, and artificial structures like wave breakers. Each specimen was measured for total length (TL, measured to the nearest 0.01 mm) using a digital Goobay caliper (0.01 mm) and total weight (TW, measured to the nearest 0.001 g) using a precision balance Cobos Complet AJ-220CEN (0.001 g). Freshly collected specimens had their gonads dissected by making a small incision on the mantle at the posterior part of the foot using a scalpel (Cañizares et al. 2021).

Sex determination was based on gonadal pigmentation following the method described by Orton et al. (1956) Additionally, a subsample of 49 mature female gonads of *P. aspera* (41.87 ± 4.33 mm total shell length, SL) and 75 of *P. crenata* (46.64 ± 5.72 mm SL) were preserved in Roti-Histofix ECO PLUS for histological analysis (Vasconcelos, Ferro, et al. 2023; Vasconcelos, Sousa, et al. 2023). Gonadal maturation stages were categorized macroscopically based on the increase in gonadal volume within the haemocoel, ranging from rudimentary virgin stage or resting after discharge of gametes (Stage I, inactive) to fully developed occupying the entire haemocoel (Stage V) (Orton et al. 1956).

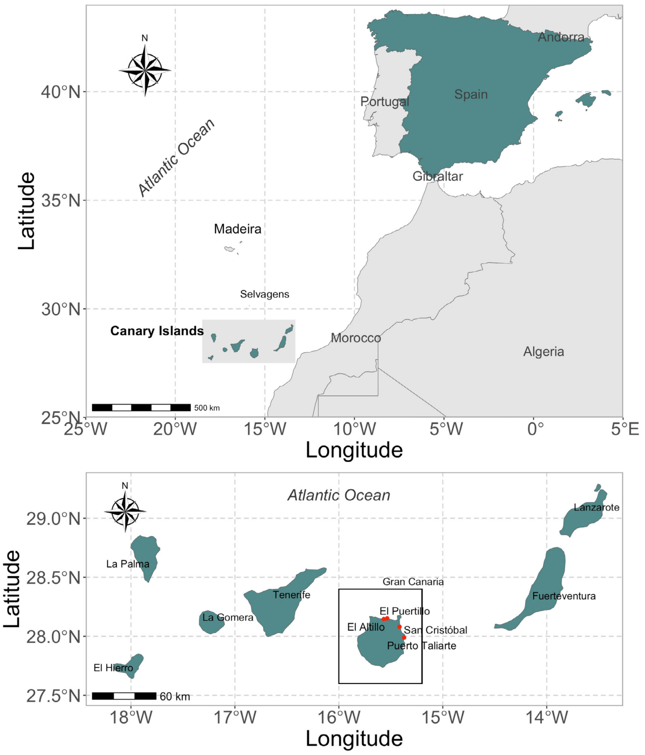

FIGURE 1 | Map presenting the geographical position of the Canary Islands in the NE Atlantic and the four sampling locations in Gran Canaria for *Patella aspera* and *P. crenata*: two on the North coast of the Island (El Altillo and El Puertillo) and two on the East coast (Puerto de Taliarte and San Cristóbal).

2.3 | Histological Analysis

Standard histological methods were employed for the examination of female specimens' gonads. Fixed gonads were dehydrated using the THERMO SCIENTIFIC Citadel 1000 and embedded in paraffin (TESPA PEC 3003-D). Transverse sections, 5 µm thick, were cut from each sample using the manual microtome Shandon Finesse 325. Sections were stained with hematoxylin and eosin and covered with a glass-mounted medium. High-contrast digital images were captured at 30X to 45X magnification using OPTIKA Lite View imaging software. The images were taken with a C-P8 digital USB camera (8.3 megapixels) mounted on a B-383PH phase contrast microscope and an SZO-T Trinocular stereozoom microscope head attached to the ST-156 base, all from OPTIKA Italy. The choice of microscope depended on the area available to measure and count oocytes. Classification of oogenesis stages and oocyte types followed the methodology of Prusina et al. (2014) with adaptations from McCarthy et al. (2008) and Belkhodja et al. (2011). Oocyte types were categorized as previtellogenic (PO; small, undifferentiated oocytes with a centrally located nucleus and scant cytoplasm), vitellogenic (VO; larger oocytes undergoing yolk deposition with increased cytoplasmic volume and more advanced cellular differentiation), and atresic oocytes (AO; degenerating oocytes characterized by disrupted structure, irregular shape, and cytoplasmic degradation). The gonadal developmental stages identified were inactive, early active, late active, ripe, atresic, spawning, and spent.

2.4 | Fecundity Type

Fecundity analysis was conducted on 45 females of *P. aspera* (41.24 ± 4.03 mm total shell length, SL) and 66 females of *P. crenata* (46.90 ± 5.79 mm SL), following criteria originally established for fish (Hunter et al. 1992; Murua et al. 2003) but successfully applied to limpets by Vasconcelos, Ferro, et al. (2023) and Vasconcelos, Sousa, et al. (2023), demonstrating their relevance to molluscan reproductive studies. Ramirez-Llodra (2002) highlights the importance of adapting fecundity assessment methods to the reproductive characteristics of each species, particularly for broadcast spawners and brooders. These criteria include (i) presence or absence of a hiatus between previtellogenic (PO) and VO; (ii) number of VO during the spawning season; (iii) mean size of VO throughout the spawning season; and (iv) incidence of atresia over the spawning period. The number and size of oocytes were recorded from 3834 PO (1313 *P. aspera* and 2521 *P. crenata*) and 12,088 VO (5575 *P. aspera* and 6513 *P. crenata*) using the ImageJ software v1.53r (http://imagej.nih.gov/ij/) (Schneider et al. 2012). The relative intensity of atresia, defined as the percentage of VO undergoing atresia relative to total number of normal oocytes in the ovary (a common procedure in fish studies; Hunter and Macewicz 1985), was estimated from histological sections of 40 *P. aspera* gonads (two in late active, 30 in ripe, and eight in the spawning stage) and 49 gonads of *P. crenata* (seven in late active, 27 in ripe, and 15 in spawning stage). Gonads in atresic stage were excluded to avoid inaccuracies caused by the predominance of oocytes in atresia. Additionally, the prevalence of atresia was examined, defined as the proportion of females with oocytes in atresia among the total number of females (Vasconcelos, Ferro, et al. 2023; Vasconcelos, Sousa, et al. 2023).

2.5 | Data Analysis

A binomial generalized linear model (GLM) was fitted using the “glm” function to analyze the proportion of male to female individuals depending on Orientation (East vs. North) and Substrate type (artificial vs. natural), and their interactions were factors included in the model.

The gonadosomatic index (GSI) for females of both *P. aspera* and *P. crenata* was calculated following the method described by Devlaming et al. (1982): $\mathrm{GSI} = 100 * (\mathrm{GW}/\mathrm{TW})$, where GW is the gonad weight (in g) and TW the total body wet weight (in g).

Differences in mean number and size of oocytes were tested across months, maturity stages, orientation (East vs. North) and substrates (artificial vs. natural). Normality of data distribution was assessed using the Shapiro–Wilk test and homogeneity of variances was checked using Levene's test. Parametric Welch's Two Sample t-test (*stats* R package; R Core Team 2024), were applied when normality assumptions were met. Non-parametric Mann–Whitney *U* tests (*U* test) were used when normality assumptions were not satisfied for comparisons between two samples. The non-parametric

TABLE 1 | Total shell length (SL, mm) and total weight (TW, g) of females (F) and males (M) of *Patella aspera* and *P. crenata* sampled according to island orientations (East vs. North) and substrate types (artificial vs. natural) of Gran Canaria between September 2023 and March 2024. *N*, Number of limpets; SD, standard deviation.

Species	Factor (orientation/substrate)	Sex	*N*	Mean SL ± SD	Mean TW ± SD
P. aspera	East	F	82	40.39 ± 5.12	8.85 ± 3.57
		M	39	40.33 ± 3.95	8.03 ± 3.22
	North	F	77	40.12 ± 4.89	8.81 ± 3.26
		M	62	41.14 ± 4.84	9.43 ± 4.39
P. crenata	East	F	66	43.45 ± 5.00	9.29 ± 3.52
		M	107	43.31 ± 4.67	8.15 ± 3.51
	North	F	70	47.14 ± 6.99	10.11 ± 3.87
		M	91	44.69 ± 5.84	8.08 ± 3.57
P. aspera	Artificial	F	13	43.91 ± 5.21	9.11 ± 4.50
		M	32	42.06 ± 4.25	8.69 ± 3.84
	Natural	F	146	39.93 ± 4.86	8.81 ± 3.32
		M	69	40.26 ± 4.55	8.98 ± 4.13
P. crenata	Artificial	F	32	47.28 ± 6.69	9.29 ± 3.39
		M	72	44.26 ± 5.24	6.96 ± 3.02
	Natural	F	104	44.76 ± 6.17	9.84 ± 3.82
		M	126	43.77 ± 5.31	8.78 ± 3.64

TABLE 2 | Results of the generalized linear model (GLM) examining the effects of orientation (East vs. North) and substrate type (artificial vs. natural) on the sex proportion in *P. aspera* and *P. crenata*. Significant effects are highlighted in bold.

	P. aspera		*P. crenata*	
Source of variation	***Z***	***p***	***Z***	***p***
Orientation	0.177	0.8594	−1.227	0.2200
Substrate type	−4.185	**< 0.001**	−2.571	**0.0102**
Orientation × substrate	1.985	**0.0471**	3.874	**< 0.001**

Kruskal–Wallis rank sum test (*KW* test) was employed to assess differences across month and maturity stages (three or more samples). Pairwise comparisons between substrates at each location were conducted using the post hoc Dunn test, with Bonferroni adjustment. The relative intensity of atresia across months was compared using the *KW* test.

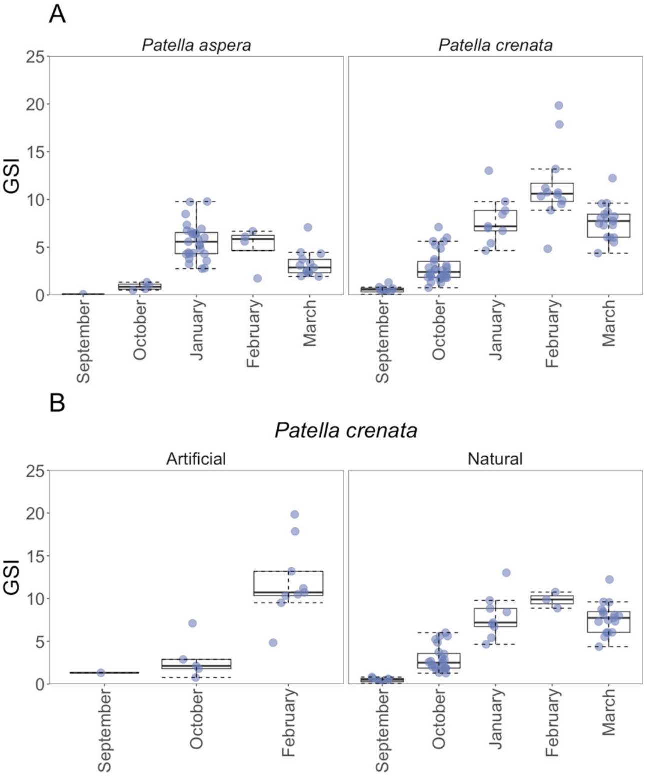

FIGURE 2 | Gonadosomatic Index (GSI) estimates for females of Patella aspera and *P. crenata* collected from Gran Canaria, NE Atlantic Ocean, from September 2023 to March 2024. (A) Monthly GSI estimates of *P. aspera* and *P. crenata* collected across all substrates. (B) Monthly GSI estimates for *P. crenata* comparing natural and artificial substrates. Boxplots represent the range (minimum to maximum), interquartile range (25th to 75th percentile), median, and outliers. *Note: P. aspera* samples from artificial substrates were only collected in February.

All statistical analyses were performed in the R environment v.4.4.1 (R Core Team 2024) using the following packages: *broom* v.1.0.5 (Robinson et al. 2023) for Shapiro–Wilk test; *car* v.3.1-2 (Fox and Weisberg 2019) for Levene's test; *dunn.test* v.1.3.5 (Dinno 2024) for pairwise comparisons; and *stats* (R Core Team 2024) for GLM, Welch's *t*, U, and KW tests.

3 | Results

3.1 | Sex Ratio and GSI

Among the 288 *P. aspera* specimens examined, 159 were females (mean shell length 40.26 ± 5.00), 101 males (40.83 ± 4.52), and 28 were classified as undifferentiated (36.52 ± 2.89) (Table 1). For *P. crenata*, out of 364 specimens, 136 were females (45.35 ± 6.36), 198 males (43.95 ± 5.27), and 30 were classified as undifferentiated (41.42 ± 5.98) (Table 1). Shell length differences were notably influenced by substrate type and geographic orientation. Specifically, *P. aspera* exhibited significantly larger shell lengths on artificial substrates (*U* test: $W = 7557$, $p < 0.001$) compared to natural ones. However, no significant variation in shell lengths was observed among different orientations for this species ($W = 9569.5$; $p = 0.261$). In contrast, the northern population of *P. crenata* displayed significantly larger shell lengths compared to other populations ($W = 12{,}252$, $p < 0.001$), underscoring the impact of geographic orientation on this species.

Significant variation in the proportion of males to females was observed for both *P. aspera* ($\chi^2 = 12.496$, p value < 0.001) and *P. crenata* ($\chi^2 = 11.141$, p value < 0.001). A GLM revealed a significant effect of substrate type on sex proportion, with natural substrates exhibiting a higher proportion of females compared to artificial substrates in both species (Tables 1 and 2). However,

TABLE 3 | Mean total shell length (mm) of *Patella aspera* and *P. crenata* females sampled from different type of substrate (platform, rocks, and wave brakers) on the East and North coasts of Gran Canaria between September 2023 and April 2024. *N*, number of limpets; SD, standard deviation; Min–Max, minimum and maximum total shell length.

Species	Orientation	Substrate type	N	Mean ± SD	Min–Max
Patella aspera	East	Platform	7	39.4 ± 3.28	33.7–42.8
		Rocks	19	42.2 ± 4.31	32.9–50.1
	North	Platform	7	39.0 ± 2.65	34.7–42.0
		Rocks	10	41.8 ± 4.09	37.7–49.4
		Wave breakers	2	43.2 ± 5.73	39.1–47.2
Patella crenata	East	Platform	3	46.8 ± 5.19	43.5–52.8
		Rocks	31	44.8 ± 5.33	34.3–53.1
		Wave breakers	1	45.8	45.8
	North	Platform	10	48.6 ± 6.25	39.2–56.8
		Rocks	10	48.8 ± 5.23	43.0–56.7
		Wave breakers	11	49.6 ± 6.32	42.0–59.3

no significant effect of orientation (East vs. North) on the sex proportion was found (Tables 1 and 2).

The GSI exhibited a seasonal trend, increasing from September to January for *P. aspera* females and from September to February for *P. crenata* females, followed by a decline in March (Figure 2A). Peak GSI values were recorded in January for *P. aspera* (5.73 ± 1.81) and in February for *P. crenata* (11.5 ± 3.98). Additionally, monthly GSI values were consistently higher for *P. crenata* compared to *P. aspera*. GSI values for *P. crenata* on both artificial and natural substrates increased from September to February, with a subsequent decline in March (Figure 2B). In

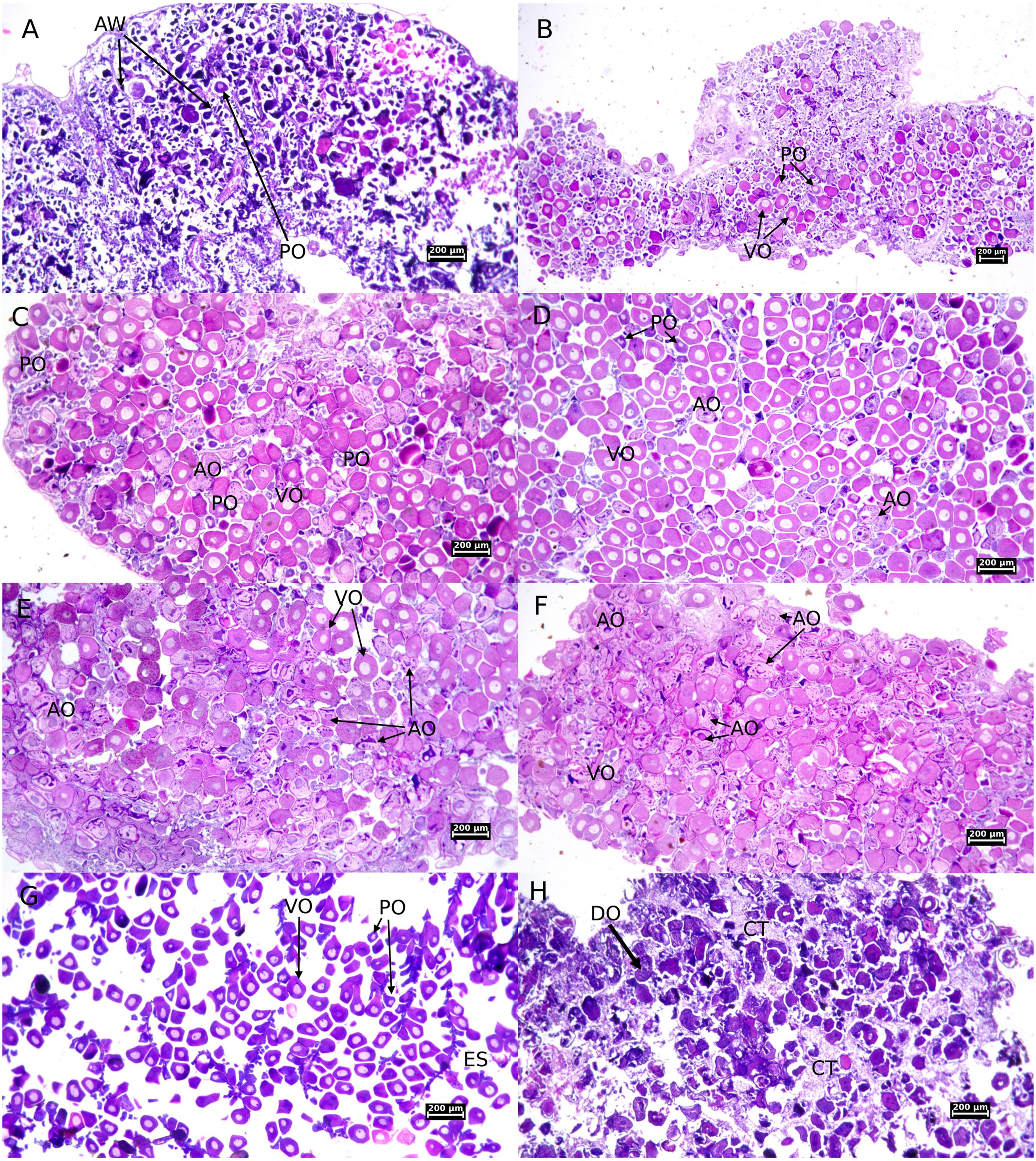

FIGURE 3 | Transverse sections of gonads of the limpet *Patella crenata* captured on the northern coast of Gran Canaria, illustrating various maturity stages: early active (A), early to late active (B), late active (C), ripe (D), atresic (E, F), spawning (G), and spent (H). AO, atresic oocyte; AW, acinus wall; CT, connective tissue; DO, degenerative oocyte; ES, empty space; PO, previtellogenic oocyte; VO, vitellogenic oocyte. *Note:* Atresic oocytes are actively undergoing degeneration and can appear across various maturation stages, while degenerative oocytes are typically present during the spent stage. The scale bar represents 200 µm. Image B was taken at 30X magnification, while all the others taken at 45X magnification.

February, GSI values were higher on artificial substrates compared to natural substrates.

3.2 | Histological Analysis

Both orientation and substrate types were considered for histological analysis (Table 3). However, due to data limitations, females of *P. aspera* from the artificial substrate wave breakers on the East coast of Gran Canaria could not be obtained. Consequently, subsequent substrate-specific analyses were restricted to *P. crenata* from the northern coast of the island, where sample sizes were sufficient ($n > 10$).

Both *P. aspera* and *P. crenata* exhibited similar developmental patterns in female gonads throughout the study period, characterized by two types of oocytes cohorts: previtellogenic and vitellogenic (Figure 3). Histological examination revealed the presence of all stages of gonadal maturity during the study period (Figure 3). Throughout this period, a subset of oocytes underwent lysis and progressed through stages of atresia.

Mature limpets were consistently present across all sampling months (Figure 4). In *P. aspera*, gametogenesis started before October, with 50% of females in the late active stage by October. For *P. crenata*, gametogenesis began in September, with 48% of females in the early active stage. By January and February, over 85% of gonads were in the Ripe stage for both species. Toward the end of the spawning season, the atresic stage became more prevalent for *P. aspera* (10%), while in *P. crenata*, atresic gonads were more prevalent earlier in the season (35%). Spawning gonads were exclusively found in March, ranging from 78% in *P. aspera* to 100% in *P. crenata* (Figure 4).

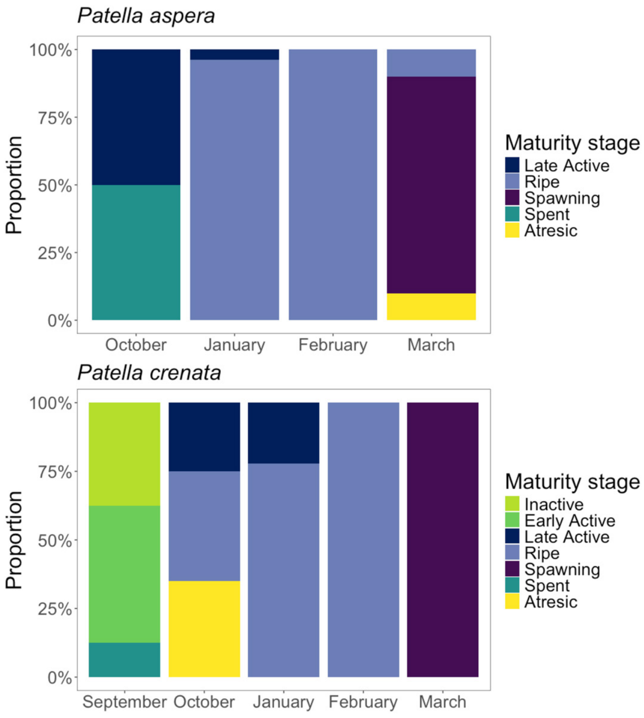

FIGURE 4 | Monthly variation of the different gametogenic stages in *Patella aspera* and *P. crenata* collected from September 2023 to March 2024 in Gran Canaria (NE Atlantic Ocean).

3.3 | Fecundity Strategy

The homogeneity of variance and normality distribution for the number and size of PO and VO were assessed for both *P. aspera* and *P. crenata*. In both species, only the number of VO exhibited a normal distribution (Shapiro–Wilk test: $p > 0.05$) (Table S1). For *P. aspera*, Levene's test indicated non-significant result ($p > 0.05$) for both the number of PO and VO, suggesting homogeneous variances (Table S2). Similarly, for *P. crenata*, the number of VO and size of PO demonstrated homogeneity of variances ($p > 0.05$).

The analysis of oocytes size frequency distribution did not reveal a hiatus between PO and VO in any sampled months for either *Patella* species (Figure 5). However, two distinct cohorts were clearly discernible: one comprising PO and the other, more advanced group, comprising VO. Throughout the sampling period, a dominant cohort in the oocyte size frequency distribution progresses, with the number of PO decreasing from October to February. PO sizes ranged from 20 to 92 μm (mean ± SD: 47 ± 14 μm; $n = 1313$) for *P. aspera* and 20 to 96 μm (46 ± 15 μm; $n = 2521$) for *P. crenata*. VO sizes varied between 67 and 214 μm (122 ± 19 μm; $n = 5575$) for *P. aspera* and 69 to 203 μm (119 ± 17 μm; $n = 6513$) for *P. crenata* (Figure 5).

Reproductive activity in *P. aspera* and *P. crenata* shows distinct seasonal patterns, as indicated by changes in oocyte number and size. From October to February, the average number of PO decreased, followed by an increase in March (Figure 6A,E and Table S3). Moreover, the VO increased in number from October to January, peaking in February before declining (Figure 6B,F). Similarly, PO sizes increased steadily from October to February and then dropped in March for both species (Figure 6C,G). VO sizes followed a similar pattern, increasing until January and decreasing by March (Figure 6D,H and Table S3). These monthly fluctuations were statistically significant, with pairwise comparisons showing notable differences between months ($p < 0.001$).

When examining the reproductive maturity stages, both *Patella* species displayed similar trends in oocyte dynamics. During the Ripe stage, the number of PO reached its lowest point for both species, coinciding with the highest levels of VO (Figure 7A,B,E,F and Table S3). In the Spawning stage, the sizes of VO decreased, and PO sizes were also smaller for both species (Figure 7C,D,G,H).

The oocyte number and size of *P. aspera* and *P. crenata* were significantly influenced by both island orientation and substrate type. On the East coast of Gran Canaria, the average number of PO was higher for both species compared to the North coast; however, these oocytes were smaller in size on the East coast (Figure 8A,C,E,G). In contrast, the average number of VO was greater on the North coast for both *Patella* species, with *P. aspera* exhibiting notably larger VO sizes on the North coast, while *P. crenata* had slightly larger VO sizes on the East coast (Figure 8B,D,F,H). Additionally, substrate type played a crucial role, with artificial substrates showing a lower average number of PO ($t = -2.08$, $p = 0.069$; Figure 9A) but a higher average number of VO ($W = 63$, $p = 0.156$; Figure 9B) for *P. crenata*. This pattern was associated with larger PO sizes ($W = 79{,}480$, $p < 0.001$;

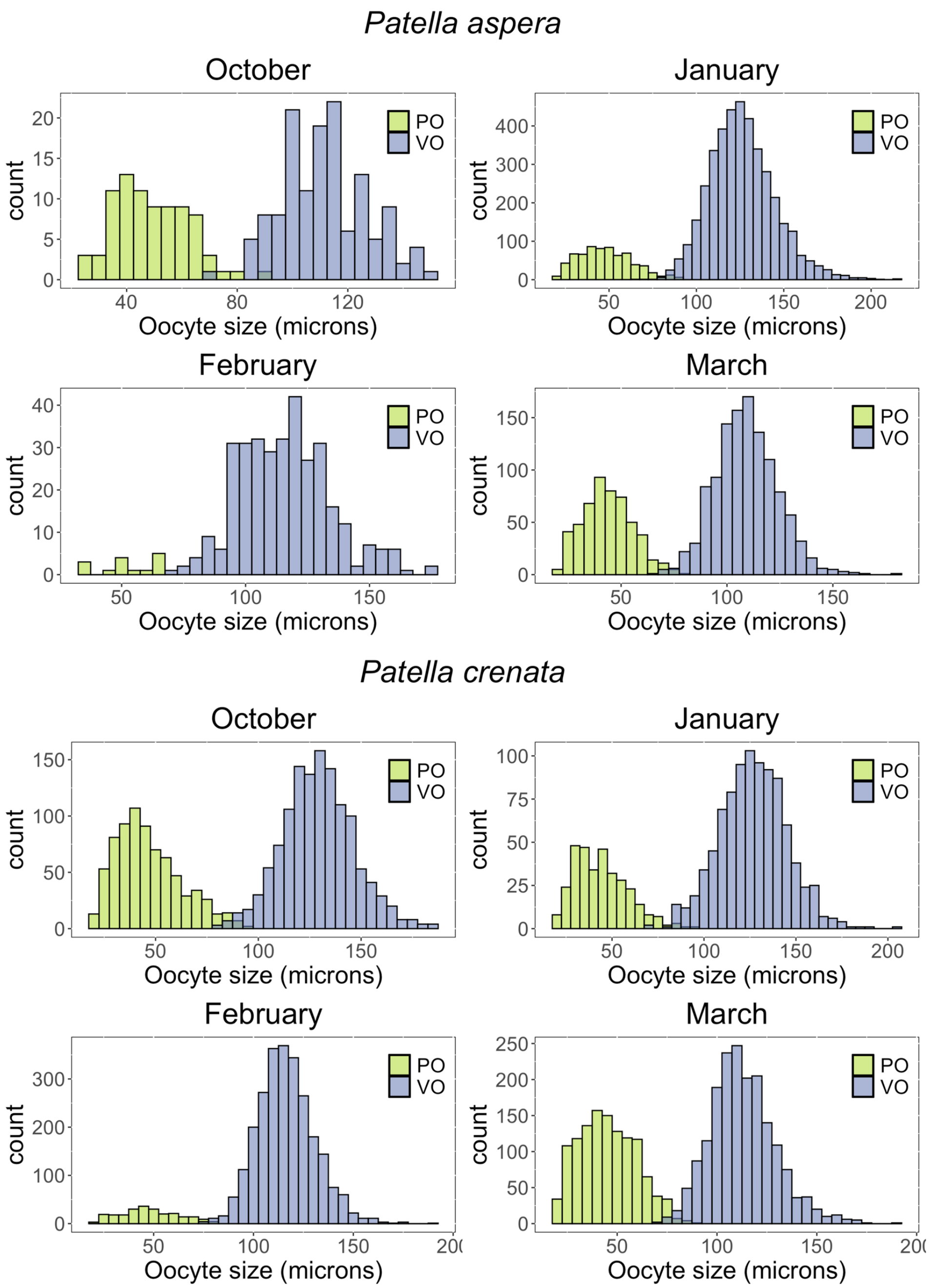

FIGURE 5 | Oocyte size frequency distribution in the limpets *Patella aspera* and *P. crenata* sampled from October 2023 to March 2024 in Gran Canaria (NE Atlantic Ocean). PO, previtellogenic oocytes; VO, vitellogenic oocytes.

Figure 9C) and smaller VO sizes ($W = 1{,}163{,}326$, $p = 0.004$; Figure 9D) on artificial substrates.

The monthly relative intensity of atresia decreased from January (10%) to March (3%) for *P. aspera* ($H = 10.20$, $p = 0.017$; Figure 10A) and from October (29%) to March (3%) for *P. crenata* ($H = 33.83$, $p < 0.001$; Figure 10B).

4 | Discussion

Our study provides significant insights into the fecundity strategies of *P. aspera* and *P. crenata* from the Canary Islands, highlighting the crucial role that substrate type plays in influencing reproductive dynamics, with natural substrates supporting a higher proportion of females and artificial substrates leading to a higher GSI in *P. aspera* and in *P. crenata*. Furthermore, both species exhibited determinate fecundity with synchronous spawning, as evidenced by the progression of dominant oocyte cohorts and corresponding changes in oocyte size and number throughout the spawning season.

The practical implications of our findings for coastal management are paramount. Incorporating fecundity data into management practices can provide a more comprehensive understanding of population dynamics and enhance the effectiveness of conservation strategies. Recognizing the higher reproductive output of *P. crenata* in artificial substrates can

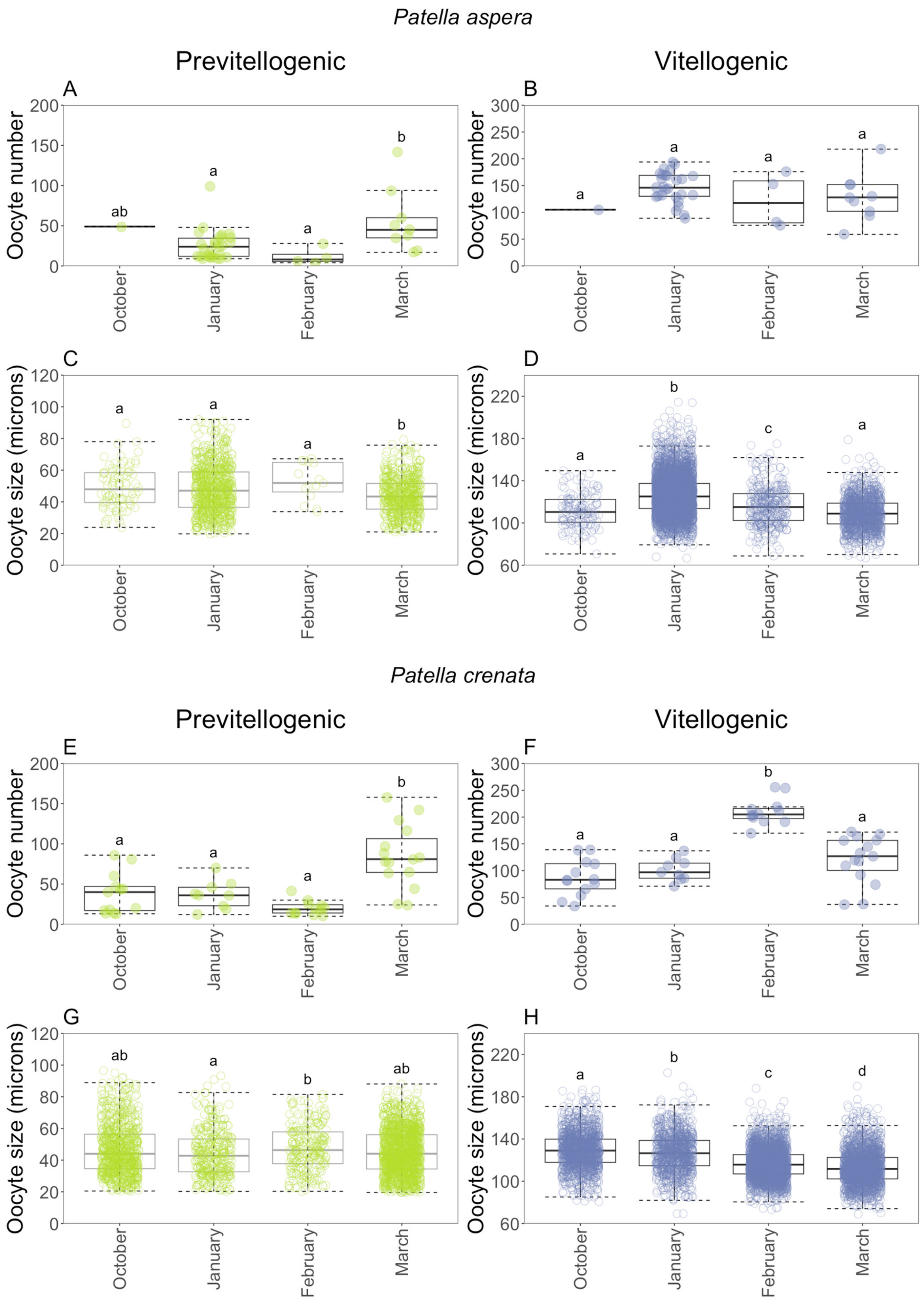

FIGURE 6 | Legend on next page.

FIGURE 6 | Monthly variation in the number (A, B, E, F) and size (C, D, G, H) of previtellogenic and vitellogenic oocytes of *Patella aspera* and *P. crenata* sampled in Gran Canaria (NE Atlantic Ocean). Boxplots display the range (minimum to maximum), the 25th percentile, the median and the 75th percentile of the data. Different letters represent significant differences between months ($p < 0.001$).

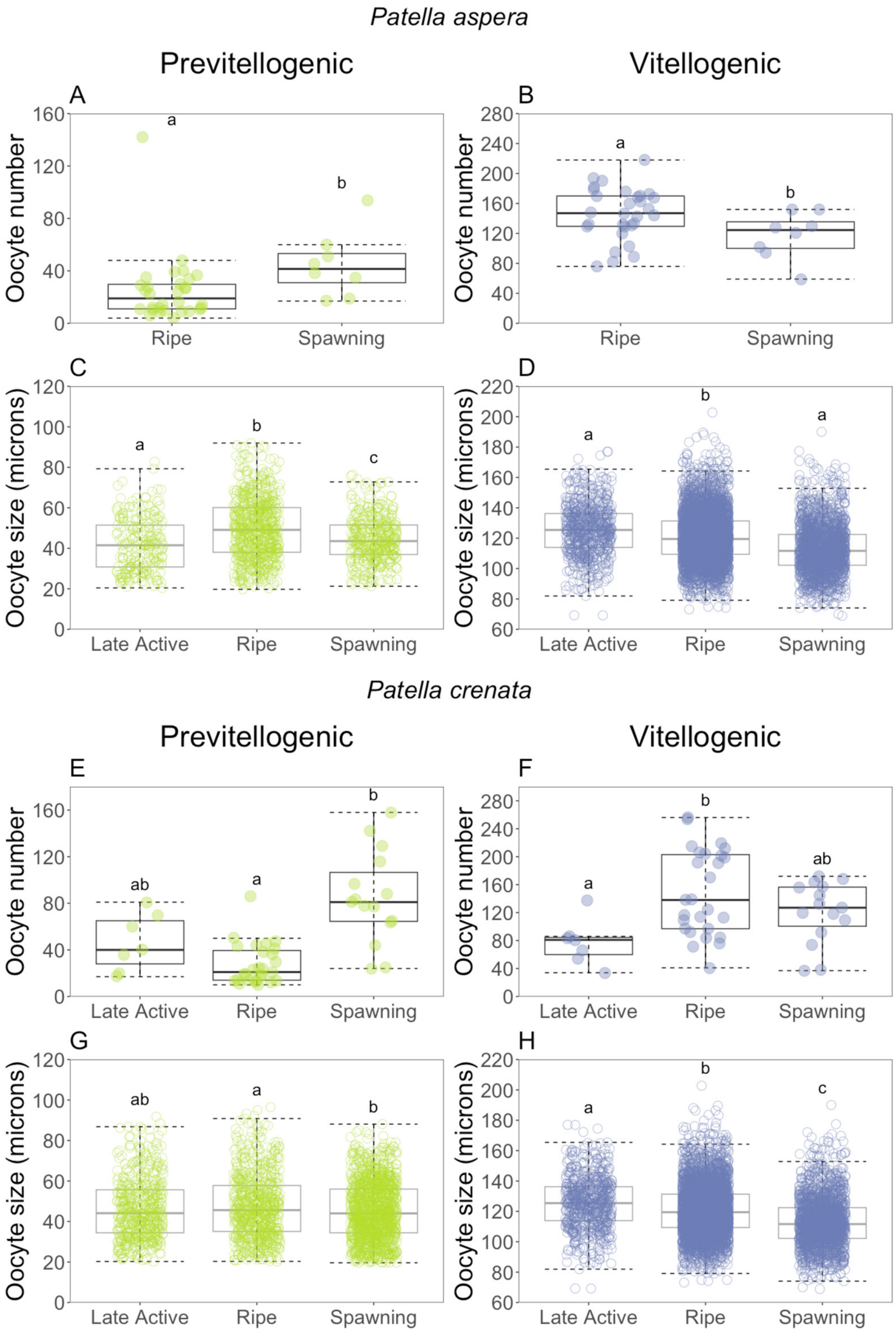

FIGURE 7 | Number (A, B, E, F) and size (C, D, G, H) of previtellogenic and vitellogenic oocytes per maturity stages of *Patella aspera* and *P. crenata* sampled in Gran Canaria (NE Atlantic Ocean). Boxplots display the range (minimum to maximum), the 25th percentile, the median and the 75th percentile of the data. Different letters represent significant differences between maturity stages ($p < 0.001$).

inform the design and placement of these structures to support limpet populations. However, the lower proportion of females in these environments suggests the need for additional measures, such as habitat restoration and protection of natural substrates, are necessary to ensure sustainable populations. The observed differences in GSI and female proportions between natural and artificial substrates underscore the need for a nuanced approach to managing coastal environments. Moreover, enforcing a closed season during the breeding period does not necessarily enhance reproductive output and has minimal effects on yield if total annual fishing effort remains unchanged (Arendse et al. 2007). Post-closed season, size-selective harvesting predominantly targets the largest individuals, mainly females of the protandric hermaphrodite species *P. aspera*, as a fraction of males' transition to females upon reaching sexual maturity (Espinosa et al. 2006, 2009; Martins et al. 2017; Sousa et al. 2019; Orton et al. 1956). The size limit management strategy, setting a minimum harvesting size of 45-mm shell length to protect part of the spawning stock, still leaves a portion vulnerable to fishing pressure (Lavin et al. 2021; Liu et al. 2016). This reduces reproductive output, which increases hyperallometrically with size and age (Barneche et al. 2018; Hixon et al. 2014; Vasconcelos, Ferro, et al. 2023; Vasconcelos, Sousa, et al. 2023). These issues should be considered when creating new management measures for limpet harvesting. Effective conservation strategies should address the specific reproductive needs and challenges of target species, aiming to support balanced sex ratios and high reproductive output.

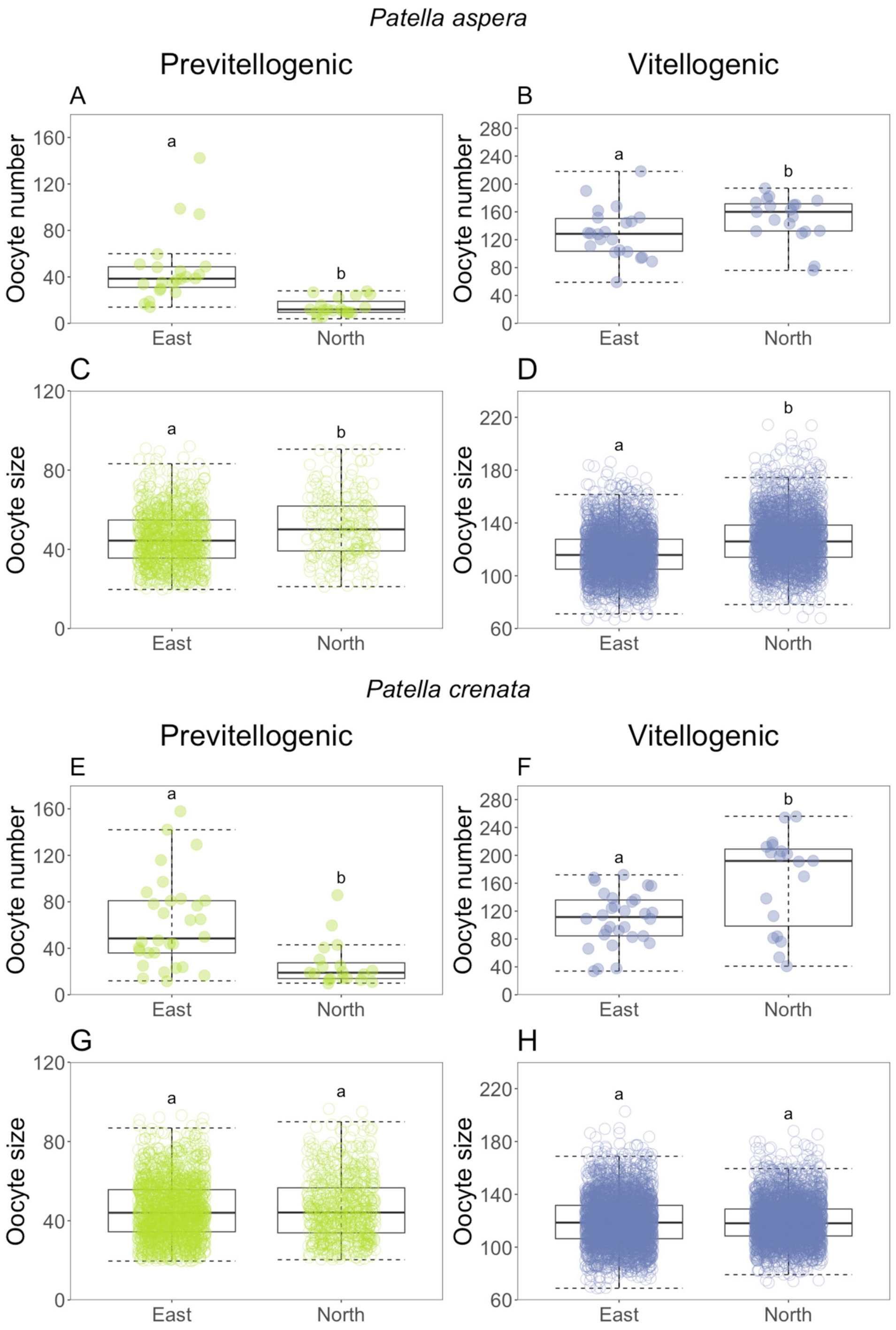

FIGURE 8 | Oocyte Number (A, B, E, F) and size (C, D, G, H) per substrate orientation of *Patella aspera* and *P. crenata* sampled in Gran Canaria (NE Atlantic Ocean). Boxplots display the range (minimum to maximum), the 25th percentile, the median, and the 75th percentile of the data. Different letters represent significant differences between orientation ($p < 0.05$).

Substrates orientation (East vs. North) plays a pivotal role in reproductive dynamics of *P. aspera* and *P. crenata*. Artificial substrates possess unique characteristics that significantly influence the reproductive strategies of these *Patella* species. Our study found that females *of P. crenata* recorded significantly higher GSI values on artificial substrates in February, suggesting that these environments may enhance reproductive vigor. This increased reproductive output may be linked to the larger shell lengths observed in the northern population of *P. crenata* compared to other populations. The North coast, subjected to greater wave action due to prevailing oceanic currents and winds entering through the north-northeast coast of the island (Riera and Delgado 2019), and artificial substrates, typically constructed in high wave energy habitats to protect human structures (Hall 2017), provide unique environmental conditions that influence these species' adaptations. Limpets from these wave-swept shores have evolved a more oval shell shape with flattened, posteriorly wider, and anteriorly pointed shells (Martínez-Ruiz et al. 2025). This morphological adaptation increases shell length, accommodating larger feet and muscles (Carvajal-Rodríguez et al. 2005; Sempere-Valverde et al. 2024), which enhances their attachment to substrates and resistance to dislodgement by waves (Márquez et al. 2015). A larger foot not only aids in anchorage but also provides greater accommodation for egg storage, potentially boosting fecundity in these high-energy environments. Furthermore, artificial substrates offer critical refuges from extremes of temperature, desiccation, competition, and predation (Fairweather 1988; Metaxas and Scheibling 1993; Johnson et al. 1998), which are especially important for *P. crenata*, as they occupy a higher position in the intertidal zone compared to *P. aspera*. However, the lower proportion of females on artificial substrates highlights challenges related to habitat suitability and the stress of altered environments. Despite these challenges, the presence of a higher number of VO on artificial substrates demonstrates the complex interplay between environmental factors and reproductive strategies. Our study found that the northern populations exhibited a higher number and size of VO compared to the eastern populations, highlighting the influence of local environmental conditions and substrate orientation on reproductive output (Hunter et al. 1992). Specifically, we observed substantial differences in the oocyte production and size of *P. crenata* in the northern region between artificial and natural substrates. For instance, artificial substrates had a lower number of PO and a higher number of VO, coupled with larger PO and smaller VO sizes than natural substrates. Additionally, the oocyte sizes in *P. aspera* and *P. crenata* were notably smaller than those in other species (Espinosa et al. 2006; Vasconcelos, Sousa, et al. 2023). Larger limpets tend to display greater reproductive potential but are more susceptible to harvesting, which can reduce fecundity (Honkoop and Van Der Meer 1997; Nakaoka 1994). Fecundity also varies widely within species, influenced by population density, nutrition, and the age and size of adults (Eckelbarger 1986).

The present study showed the profound impact of substrate type and orientation on the reproductive strategies and morphologies of limpets in intertidal habitats, particularly emphasizing the need for targeted conservation strategies to preserve the unique adaptations of *Patella* species along the northern shore of Gran Canaria. Future research should continue to explore these environmental factors to better understand their complex dynamics, ensuring ongoing monitoring and protection to maintain

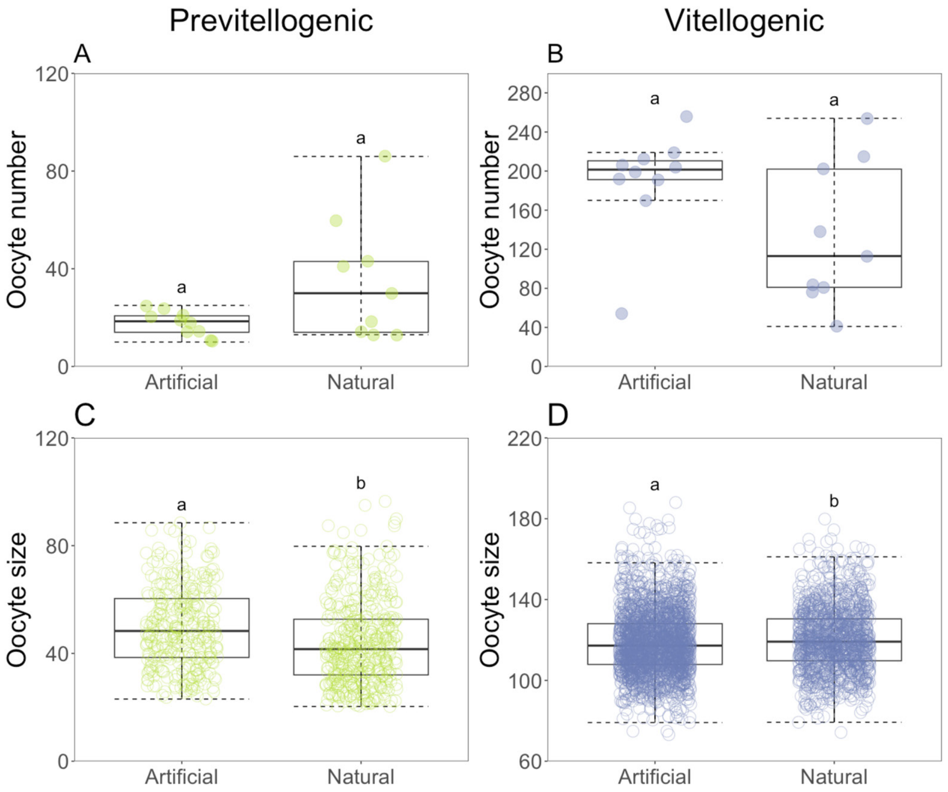

FIGURE 9 | Oocyte Number (A, B) and size (C, D) for each substrate type (artificial vs. natural) in Patella crenata specimens collected from the northern coast of Gran Canaria (NE Atlantic Ocean). Boxplots display the range (minimum to maximum), the 25th percentile, the median and the 75th percentile of the data. Different letters represent significant differences between substrate type ($p < 0.001$).

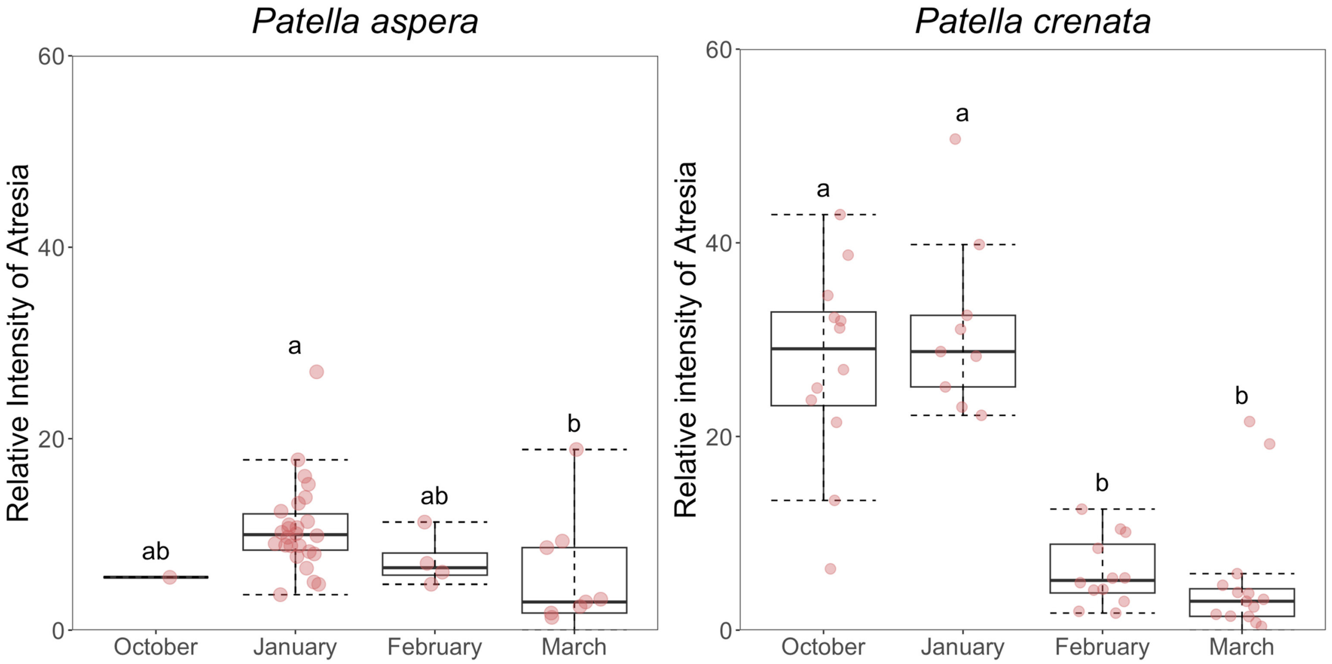

FIGURE 10 | Relative intensity of atresia estimated for *Patella aspera* and *P. crenata* sampled in Gran Canaria (NE Atlantic Ocean) from October to March. Boxplots display the range (minimum to maximum), the 25th percentile, the median, and the 75th percentile of the data. Different letters represent significant differences between substrate type ($p < 0.001$).

the diverse phenotypic traits and ecological resilience of these intertidal populations. However, these results should be interpreted with caution due to several gaps in the collected data. One major challenge is that the collection of limpets is a regulated activity requiring a special permit, and a closed season from November to April prohibits capture during the critical spawning period. Additionally, certain coastal areas are off-limits for shellfish collection year-round, further complicating the gathering of comprehensive data. Another significant limitation is that fecundity assessments are based solely on female specimens, despite the fact that a high proportion of males was observed—over 35% of the sampled *P. aspera* and > 55% of *P. crenata* between September and March. This limitation reduced the amount of data available for analysis and may have influenced our results. Furthermore, the intertidal positioning of *P. aspera* complicated collection efforts during the spawning season, which coincides with winter months when sea conditions are harsh and unpredictable. The aforementioned challenges highlight areas for improvement in future studies.

5 | Conclusions

Our study provides critical insights into the fecundity strategies of *P. aspera* and *P. crenata*, highlighting the significant influence of substrate types and environmental conditions on their reproductive dynamics. We observed notable differences between natural and artificial substrates, with higher GSI values recorded on artificial substrates during peak spawning periods. This suggests that artificial substrates may serve as important reproductive habitats for these species. These findings highlight the importance of developing conservation strategies that address the unique reproductive needs of different habitats. By incorporating fecundity data into coastal management practices, we can enhance the sustainability of limpet populations, addressing existing knowledge gaps and advancing our understanding of marine mollusk reproductive ecology. This research lays the groundwork for effective management strategies designed to protect these vital marine resources for the long term.

Future research should investigate the long-term effects of artificial substrates on limpet populations, particularly their impact on reproductive success, sex ratios, and overall population dynamics. It will also be important to explore additional factors such as food availability, predation pressures, and environmental stressors to better understand how these variables interact with substrate types to influence fecundity. Uncovering the mechanisms behind the observed differences in GSI and sex ratios between natural and artificial substrates is crucial for developing conservation strategies that are closely aligned with the needs of limpet populations. Expanding the geographical scope of research to include a variety of regions and a wide range of species will offer a more comprehensive perspective on limpet fecundity strategies. Collaborative studies across different locations can reveal both universal trends and unique adaptations, paving the path for more integrated approaches to marine mollusk conservation on a global scale.

Author Contributions

J.V.: conceptualization, methodology design, data collection, data curation, data analysis, funding acquisition, investigation, project administration, resources, supervision, validation, and writing – original draft. **P.A.:** data collection, data curation, investigation, data analysis, and writing – original draft. **O.M.R.:** data collection and data curation. **A.R.D.:** data curation. **V.M.T.:** validation and writing – review and editing. **R.R.:** conceptualization, methodology design, resources, investigation, project administration, and writing – review and editing.

Acknowledgments

We are grateful to the Directorate of Fisheries of the Government of Gran Canaria for granting permission to collect limpets between September and October of 2023 and January to March of 2024. To Prof. José Mario González Pajuelo for providing facilities and materials for the paraffin method. This document is the result of a final research project conducted as part of a Bachelor's degree, supported by the Portuguese national funds through the Fundação para a Ciência e a Tecnologia I.P. (FCT), under the project "*Metacommunity dynamics of complex life cycle species in exploited ecosystems*" (LAPACOM), grant number EXPL/MATAPL/0262/2021 (https://doi.org/10.54499/EXPL/MAT-APL/0262/2021) and through the strategic project UIDB/04292/2020 (https://doi.org/10.54499/UIDB/04292/2020) and UIDP/04292/2020 (https://doi.org/10.54499/UIDP/04292/2020) awarded to MARE and project LA/P/0069/2020 (https://doi.org/10.54499/LA/P/0069/2020) granted to the Associate Laboratory ARNET. J.V. was supported by the "Grants for the Viera y Clavijo training program for researchers" of the Government of the Canary Islands and Universidad de Las Palmas of Gran Canaria (VIERA Y CLAVIJO-2022-CIENCIAS-1).

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

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

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Supporting Information

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