Reproductive ecology studies for sustainable fisheries management in Iberoamerica.
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Life-history traits and reproductive strategies of *Pegusa lascaris* and *Buglossidium luteum* in the Ártabro Gulf

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Summary: Reproductive biology plays a key role in fish population dynamics and sustainable fisheries management. However, detailed reproductive data remain particularly scarce for many species of low commercial interest. This study investigates the biology and reproductive strategies of two sole species (*Pegusa lascaris* and *Buglossidium luteum*) in the Ártabro Gulf, NW Iberian Peninsula. Sampling was conducted quarterly between 2017 and 2024, and 203 bottom trawl hauls were taken at 13 stations (10–50 m depth). All specimens were measured for length and weight, and sex and maturity stage were recorded macroscopically. Both species showed hyperallometric growth patterns, with females dominating at larger sizes. The spawning period for *P. lascaris* occurred from May to September, whereas that of *B. luteum* occurred between March and August. Size at maturity analysis (L_{50}) revealed that *P. lascaris* matured at 133.6 mm and *B. luteum* at 80.7 mm. Gonad samples were processed histologically to confirm maturity stages and assess oocyte development. Histological examination confirmed that both species are batch spawners with asynchronous oocyte development. These results will enhance current knowledge of the biology and reproductive strategies of the two species and will significantly improve the input into the stock assessment process, particularly for *P. lascaris*.

Keywords: sole species; length-weight relationship; sex ratio; size at maturity; spawning season; ovary stages; oocyte size; NW Iberian Peninsula.

Parámetros de historia de vida y estrategias reproductivas de *Pegusa lascaris* y *Buglossidium luteum* en el golfo Ártabro

Resumen: La biología reproductiva desempeña un papel clave en la dinámica poblacional de los peces y en la gestión sostenible de las pesquerías. Sin embargo, la información reproductiva detallada sigue siendo especialmente escasa en muchas especies de bajo interés comercial. Este estudio analiza la biología y las estrategias reproductivas de dos especies presentes en el golfo Ártabro, al noroeste de la Península Ibérica (*Pegusa lascaris* y *Buglossidium luteum*). El muestreo se realizó trimestralmente entre 2017 y 2024, con un total de 203 lances de arrastre de fondo en 13 estaciones (entre 10 y 50 m de profundidad). Todos los ejemplares fueron medidos en talla y peso, registrándose el sexo y el estado de madurez en escala macroscópica. Ambas especies mostraron patrones de crecimiento hiper alométrico, con dominancia de hembras en las tallas mayores. El periodo de puesta de *P. lascaris* se extendió de mayo a septiembre, mientras que *B. luteum* presenta un periodo comprendido entre marzo y agosto. El análisis del tamaño de madurez (L_{50}) reveló que *P. lascaris* alcanza la madurez a los 133,6 mm y *B. luteum* a los 80,7 mm. Las muestras de gónadas fueron procesadas histológicamente para confirmar los estados de madurez y evaluar el desarrollo ovocitario. El análisis histológico confirmó que ambas especies son desovadoras en lotes con desarrollo ovocitario asincrónico. Estos resultados mejoran el conocimiento actual sobre la biología y las estrategias reproductivas de ambas especies y contribuirán significativamente al proceso de evaluación de stocks, especialmente en el caso de *P. lascaris*.

Palabras clave: lenguado, relación talla-peso, proporción sexual, tamaño de madurez, temporada de desove, estados de desarrollo gonadal, tamaño de ovocitos, noroeste de la Península Ibérica

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INTRODUCTION

Understanding the dynamics of a fish population requires knowledge of its life-history strategy—the suite of traits that shape an individual's reproductive patterns across its lifespan (Wootton 1993). Reproduction encompasses evolved adaptations to maximize the production of viable offspring capable of recruiting into future adult populations, thereby ensuring the species' persistence (Pianka 2000, Wootton 1990). Fishes exhibit considerable diversity in reproductive strategies (Helfman et al. 1997, 2009), shaped by key traits such as spawning frequency, oocyte recruitment dynamics, spawning periodicity and fecundity patterns. Scientists and resource managers require knowledge of life-history parameters to effectively evaluate and mitigate risks to natural populations and ecosystems (Thorson et al. 2017). Studies on reproduction, including size at maturity, fecundity, duration of reproductive season, daily spawning behaviour and spawning fraction, allow the reproductive capacity of a population to be quantified. This information, in combination with estimates of egg production, enables the estimation of spawning stock biomass (Parker 1980, Hunter et al. 1985). Life-history parameters are therefore key information for stock assessment and for ensuring the sustainable exploitation of stocks (Link et al. 2002). However, basic life-history information is often lacking for newly exploited or non-exploited species (King and McFarlane 2003).

The two target fishes in this study are members of the Soleidae family, *Pegusa lascaris* and *Buglossidium luteum*. *P. lascaris*, the sandsole, is a demersal species found in gravel, sand or mud bottoms between 5 and 350 m from the southern North Sea to the Guinean Gulf and in the Mediterranean Sea (Quéro et al. 1986). This species is captured by the trawl and trammelnet fleet (Ozyurt et al. 2018) and is of growing commercial interest. In the Atlantic Iberian waters, *P. lascaris* represents 21% of the total catches of assessed soles. In 2023, its catches represented 218 tonnes (ICES 2024). However, it is included in the stock assessment of sole (*Solea solea*) due to issues of misidentification in some ports, where it is often confused with the other two species of the Solea genus (*S. solea* and *S. senegalensis*) (Dinis et al. 2020). *B. luteum*, the solenette, is the smallest species of the family, reaching only 100–130 mm in total length (Wheeler 1969). It appears at depths of 5–450 m (Muus and Nielsen 1999) and mainly inhabits the coastal strip between the intertidal zone and the 40-m isobath (Déniel 1981). It is widely distributed across the eastern Atlantic, the North Sea, the Kattegat, the Baltic Sea and the Mediterranean Sea (Froese and Pauly 2024). Although solenette is not a target species, it is usually found as by-catch in fisheries (İlkyaz et al. 2010) and has started to be commercialized.

Despite the commercial interest of these species, there is a lack of information regarding their biology and ecology, particularly with regard to factors influencing their population dynamics and reproduction. Several biological aspects of *P. lascaris* and *B. luteum* have been studied previously, such as feeding habits (Nottage and Perkins 1983, Cabral et al. 2002), growth (including length-weight relationship) (Deniel 1990, Félix et al. 2011), spawning season (Pajuelo and Lorenzo 2008) and age (İlkyaz et al. 2010, Rodríguez-García et al. 2024). However, no reproductive study based on gonad histology was available for these species in the study area. The present paper aims to provide the first biological data on *P. lascaris* and *B. luteum* in the NW Iberian Peninsula mainly related to their reproduction. Our results improve the understanding of the biology and ecology of both species and provide key information for the assessment of their stock status.

MATERIAL AND METHODS

Sampling

The study area is the Ártabro Gulf, an area of about 1500 km^2 formed by three rias (A Coruña, Ares and Ferrol) off the NW coast of Galicia (NW Iberian Peninsula) (Fig. 1). It is a complex hydrographical area with episodic summer upwelling events (Prego and Varela 1998) resulting in high primary production (Bode and Varela 1998). The study was conducted as part of the BIGA project, with quarterly sampling over five years (2017–2018 and 2022–2024), totalling 203 hauls. Sampling consisted of a ten-minute bottom trawling haul at 2 knots with a *bou de vara* (a type of beam trawl) at 13 fixed stations located in the three rias of the Ártabro Gulf (Fig. 1). The stations were located at depths between 10 and 50 m, a range inaccessible to oceanographic vessels conducting the evaluation of fishery resources.

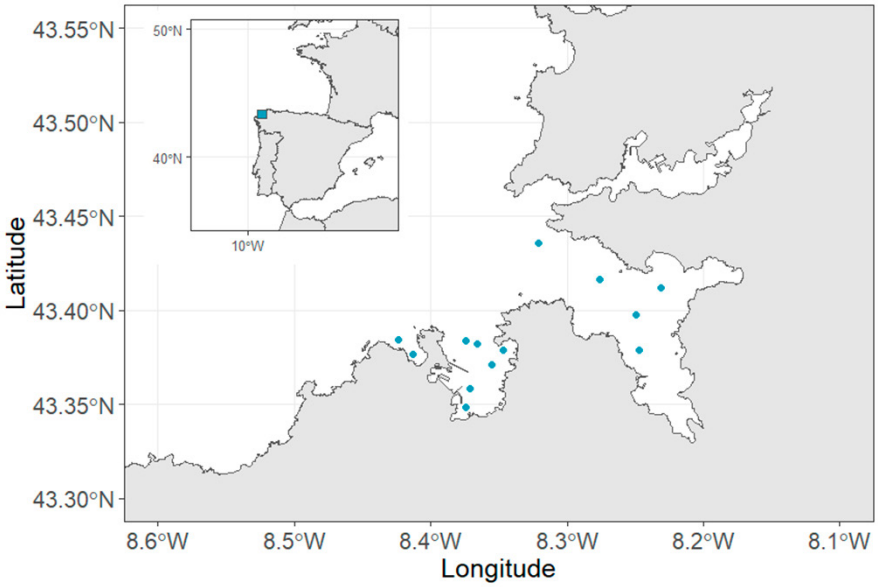

Fig 1. – The Ártabro Gulf, sampling area of the study. Blue points represent the 13 fixed stations used for collecting the individuals.

Laboratory work

All captured individuals were measured considering total length (TL, to the nearest mm) and total weight (TW, to the nearest 0.01 g). In addition, the sex and the macroscopic gonad developmental stage were recorded. Macroscopic stages were assessed considering four different maturity stages: immature, developing, spawning-capable and regressing/regenerating, based on the common maturity scale proposed in the ICES WKMATCH (in 2012; ICES 2014).

To create a collection for reproductive studies, the ovaries of some of the captured females (n=70 for *P. lascaris* and n=16 for *B. luteum*), were extracted and fixed in buffered 4% formaldehyde for at least two weeks. After fixation, a subsample of each ovary was dehydrated in a series of ethanol solutions, cleared and embedded in paraffin, sectioned at 3–4 µm and stained with Papanicolaou's haematoxylin–eosin. Histological sections were examined using a microscope to confirm macroscopic sex and maturity stage. To assess the maturity stage of the females, the developmental stages of the oocytes (Tyler and Sumpter 1996) were identified based on the most advanced follicular stage observed in histological sections. Female microscopic maturity stage was determined based on the standardized classification of Brown-Peterson et al. (2011): immature, developing, spawning-capable and the substage actively spawning, regressing and regenerating.

Since ovarian maturity in many flatfish species has been shown to not differ between positions in the ovarian lobe or between lobes (Pajuelo and Lorenzo 2008), we can assume that the histological sections and the oocyte size-frequency analysis accurately represent the gonad state from any area of either ovary without introducing sampling bias. Histological sections were used to test the macroscopic assignation of ovary stages for each species as well to identify their reproductive strategy. However, the number of histological sections was insufficient to analyse the size of first maturation or the reproductive annul cycle, which were estimated from the macroscopic maturity information. In addition, the oocyte size-frequency and the subsequent result of the type of oocyte development were determined by measuring the size of the oocytes in three actively spawning females per species. For this purpose, a subsample weighing between 20 and 40 mg, depending on the size of the oocytes, was taken from the fixed ovaries. The sample was placed in water to separate the oocytes using a washing procedure (modified from Lowerre-Barbieri and Barbieri 1993). An ultra-sonic pen was used to assist in the separation of the oocytes from the connective tissue. Once the oocytes were separated, sieves were used to select the oocytes and discard the tissue. Oocyte counts and measurements were obtained using a computer-based image analysis system.

Statistics

The length-weight (TL-TW) relationship was analysed separately for males and females and for combined sexes using the power function $TW=aTL^b$ (Le Cren 1951), where TW is body weight (in grams), TL is total length (in millimetres), 'a' is the scaling coefficient, and 'b' is the exponent. The parameters a and b were estimated by linear

regression analysis on log-transformed data. The predicted TL-TW curve was calculated and tested for statistical significance, including the interaction term (sex:TL).

The sex ratio was estimated as the proportion of females to the total number of individuals (females+males) in total and by size classes of 50 mm for *P. lascaris* and 20 mm for *B. luteum*. Differences by size classes were tested with the Pearson chi-squared test. The spawning period was established by monitoring monthly variations of the frequency of female macroscopic maturity stages, and the Kruskal-Wallis test was performed to detect significant monthly changes. The female maturity ogive was estimated using a generalized linear model with a Bernoulli distribution and a logit link function (McCullagh and Nelder 1989). Maturity classification through macroscopic examination (0=immature, 1=mature), served as the response variable, while TL was used as the explanatory variable. The maturity ogive and the corresponding length at which 50% (L_{50}) and 95% (L_{95}) of the population has become mature were calculated exclusively for females owing to the lack of gonad sampling in males.

All statistical analyses were conducted with R software version 4.4.2 (R Core Team, 2024), with significance set at $p<0.05$.

RESULTS

Of the 617 individuals of *P. lascaris* that were analysed, 256 were males, 259 females and 7 undetermined individuals (Table 1). Mean length was 191 mm and the minimum and maximum sampled sizes were 69 mm and 302 mm, respectively. The TL-TW relationship was significant ($r^2=0.97$, $p<0.001$; Fig. 2A) with a b of 3.14 (CI 3.09-3.19), and the analysis by sexes showed differences between males and females ($p<0.001$; Fig 2B). Males and females showed significant differences in the regression coefficient but not in the intercept. Both sexes showed hyperallometric growth, with b=3.20 (CI: 3.09-3.17) in males and b=3.25 (CI: 3.11-3.24) in females. Thus, females attained greater weight at the same length. The sex ratio showed a total value of 1:0.99. However, sex ratio by size classes showed significative differences ($p<0.001$), with a higher percentage of females as length increased (Fig 3.A), reaching 100% of females in sizes above 250 mm (Fig. 3B).

Table 1. – Number of sampled individuals by sex (male, female and undetermined) by months for *Pegusa lascaris* and *Buglossidium luteum*.

	P.lascaris			*B. luteum*		
Month	Male	Female	Undetermined	Male	Female	Undetermined
Feb	6	7	2	0	0	5
Mar	5	5	0	85	67	7
Apr	16	24	1	33	117	6
May	10	28	0	169	169	2
Jun	73	64	0	86	114	11
Jul	24	23	2	9	46	18
Aug	26	27	0	41	74	12
Sep	69	38	0	31	53	79
Oct	8	19	2	12	28	3
Nov	2	7	0	20	14	3
Dec	17	17	0	3	4	0
Total	256	259	7	489	686	146

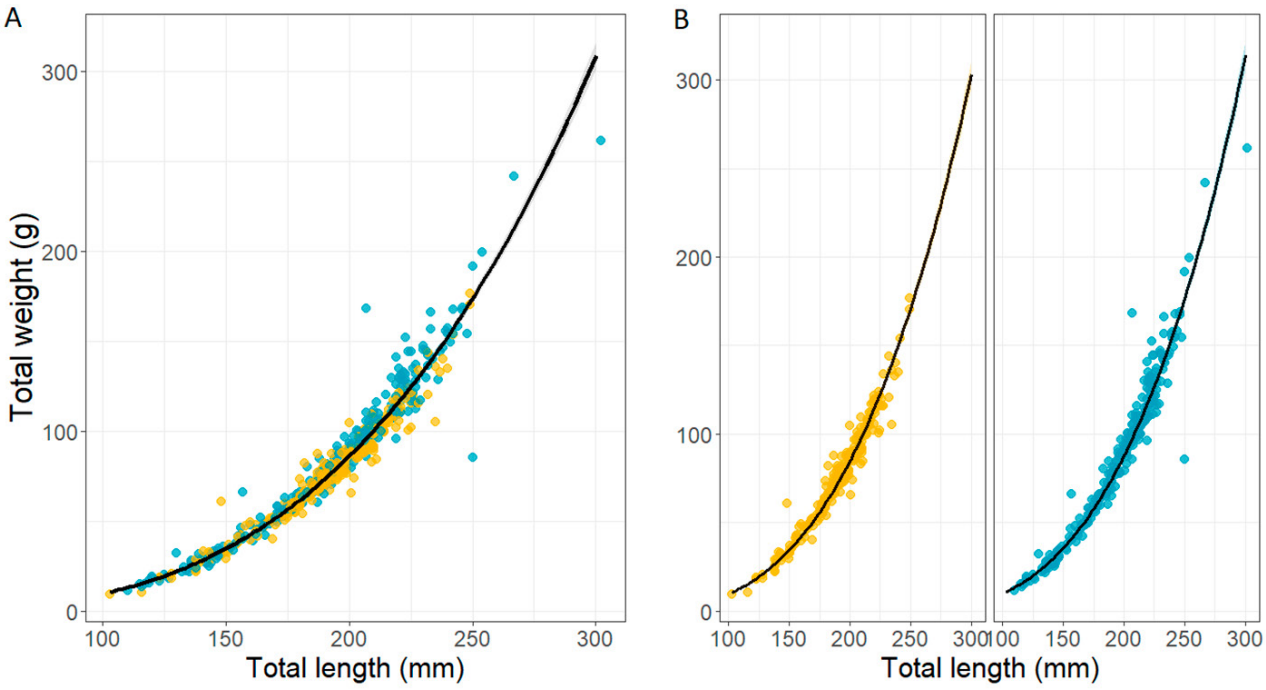

Fig 2. – A, weight–Length relationship of *P. lascaris* for combined sexes. B, weight–Length relationship of *P. lascaris* by sex. Males and females are represented by yellow and blue, respectively. Points represent the observed data and lines the prediction from the linear regression model.

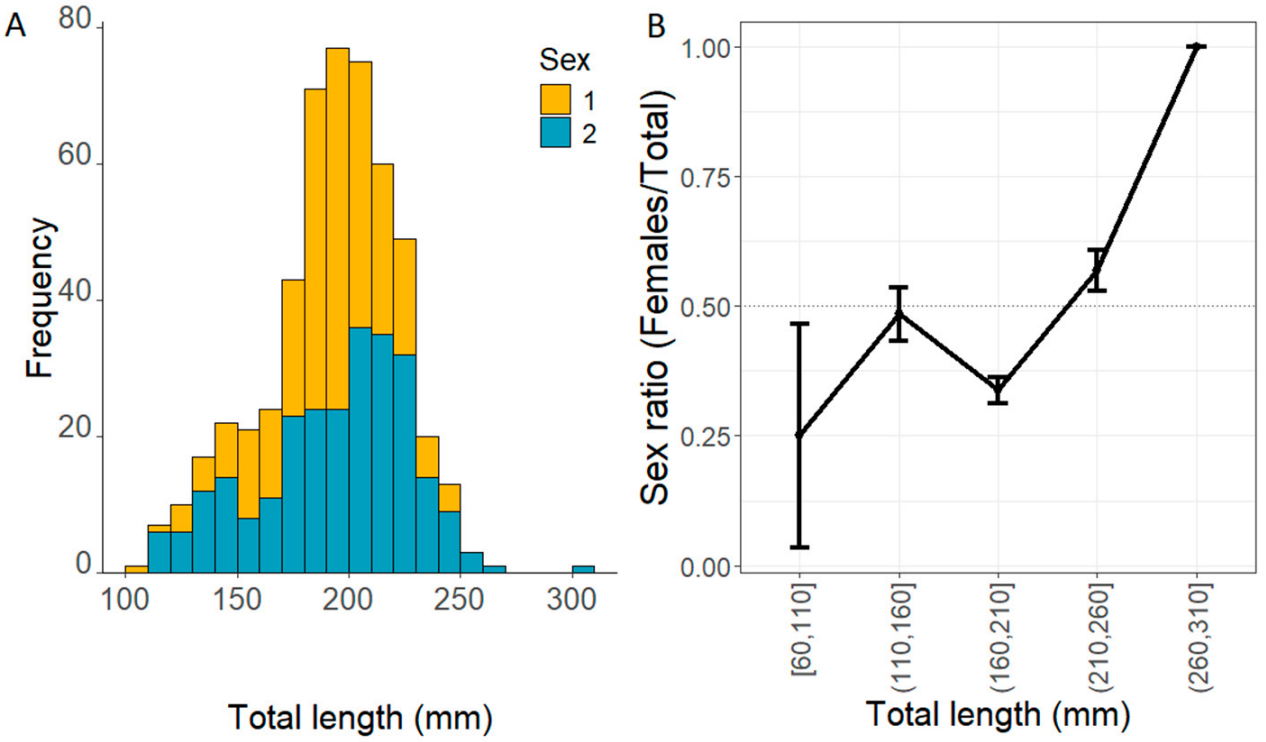

Fig 3. – A, length frequency (in mm) for males (yellow) and females (blue) individuals of *P. lascaris*. B, sex ratio, considered as the percentage of females of the total individuals, by size intervals of 50 mm.

The frequency of maturity stages varied throughout the year for males and females ($p<0.001$; Fig. 4). Developing individuals are found in almost all months. Spawning activity (spawning-capable stage) was detected only in

September for males, and from May to September for females. Immature and postspawning individuals of both sexes were collected throughout the year. The length at first maturity in females recorded in this study was 116 mm, and there was a significant relationship between length and maturity ($p<0.001$, Fig 5) with an intercept of $a=-4.54$ and a slope $b=0.03$. The predicted length at 50% maturity (L_{50}) was 133.64 mm (SE 9.63 mm), while the L_{95} was 220.35 mm (SE 10.37 mm).

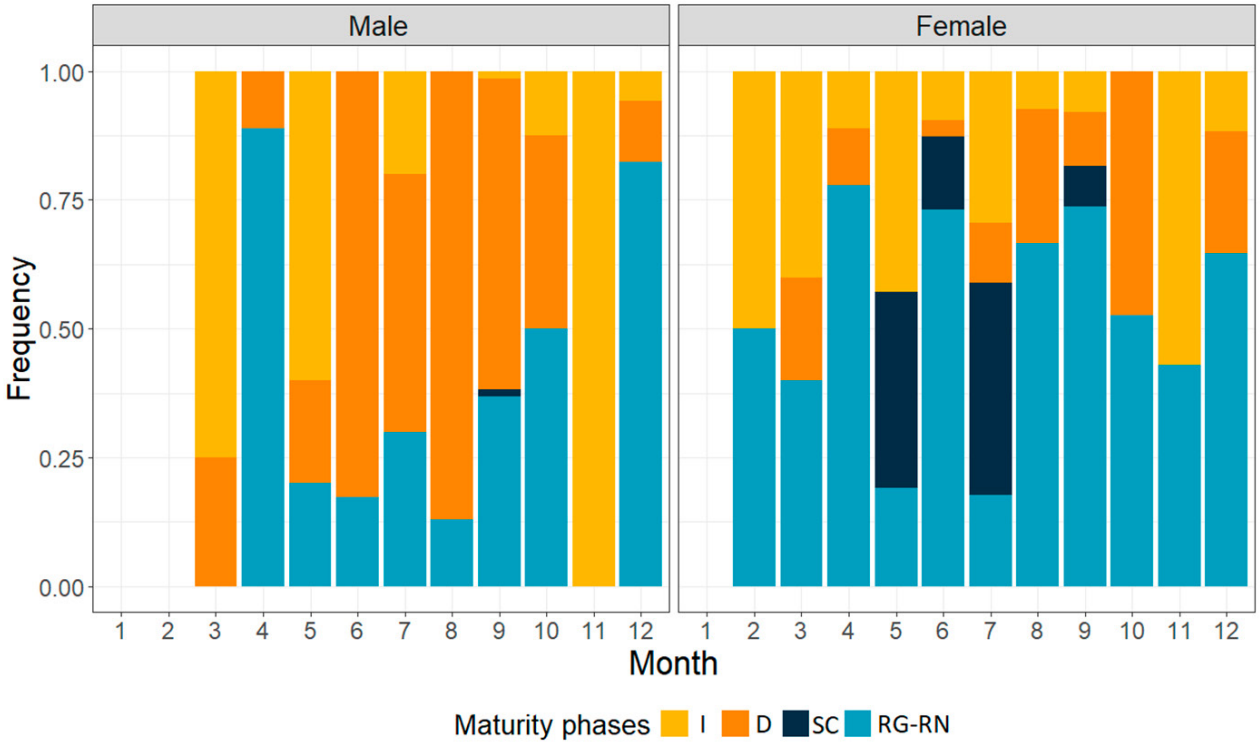

Fig 4. – Frequency distribution (as proportion) of sexually maturity stages for males and females based on the scale defined by the ICES WKMATCH (in 2012; ICES 2014): immature (I), developing (D), spawning (SC) and regressing/regenerating (RG-RN) of *P. lascaris*, captured on a monthly basis.

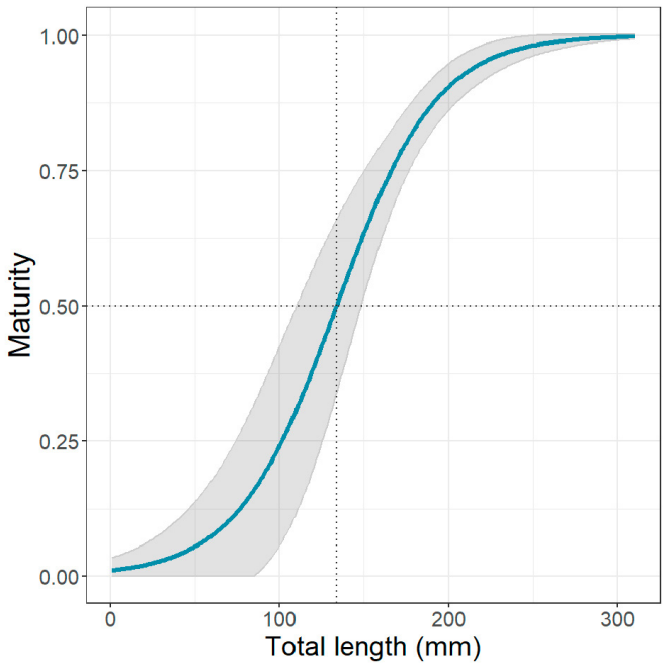

Fig. 5. – Estimated maturity ogive of *P. lascaris* females. Dotted lines represent the size at 50% maturity (L_{50}=133.64 mm).

Figure S1 shows maturity ovary stages based on the microscopic scale, from immature to regenerating females. Considering the microscopic ovary stage scale, actively spawning females were mostly in the oocyte phases, with two distinct cohorts of vitellogenic oocytes simultaneously, one in the early phase and one in a more advanced stage, as well as hydrated oocytes (a signal of imminent spawning). Additionally, postovulatory follicles were present in mature ovaries. Lastly, the oocyte size-frequency ranged between 162 and 1287 µm, with the highest occurrence of the smaller sizes. Three different modes were detected in the oocyte frequency (Fig. 6): the first one with the smallest cohort (63% of the total sample) with a range of 162–430 µm and a mean of 279 µm, the second one with oocytes with intermediate diameters (12% of the total sample) with a minimum of 440 µm and a maximum of 826 µm, and the third mode with the highest diameters (25% of the total sample), from 1064 to 1287 µm range and a mean of 1172 µm.

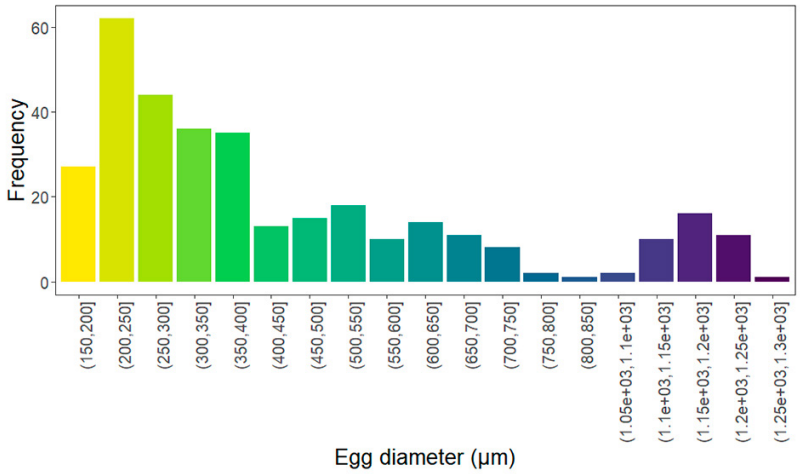

Fig. 6. – Oocyte size-frequency distribution in an actively spawning female of *P. lascaris*.

A total of 1321 *B. luteum* specimens were examined, comprising 489 males, 689 females and 146 individuals of undetermined sex (Table 1). The average body length was 92 mm, with sizes ranging from 30 mm (minimum) to 186 mm (maximum). The TL-TW relationship was significant (r^2=0.97, p<0.001; Fig. 7A), exhibiting a hyperallometric growth coefficient (b=3.19, CI 3.16–3.22). TW-TL by sex analyses revealed differences between males and females (p<0.001; Fig. 7B), with different intercepts but similar regression coefficients. Both sexes displayed hyperallometric growth. While males had a b of 3.16 (CI 3.12–3.19), females showed a slightly higher b of 3.18 (CI 3.13–3.23), indicating that females achieve greater weight at similar lengths. The overall sex ratio was less balanced (1:0.71) than in *P. lascaris*, and significant differences emerged across size classes (p<0.001). Sexual dimorphism was observed, with females reaching larger sizes than males. While males dominated in sizes <90 mm, the situation reversed in sizes >110 mm and females dominated in larger size groups, constituting more than the 80% of the largest individuals (Fig. 8A, B).

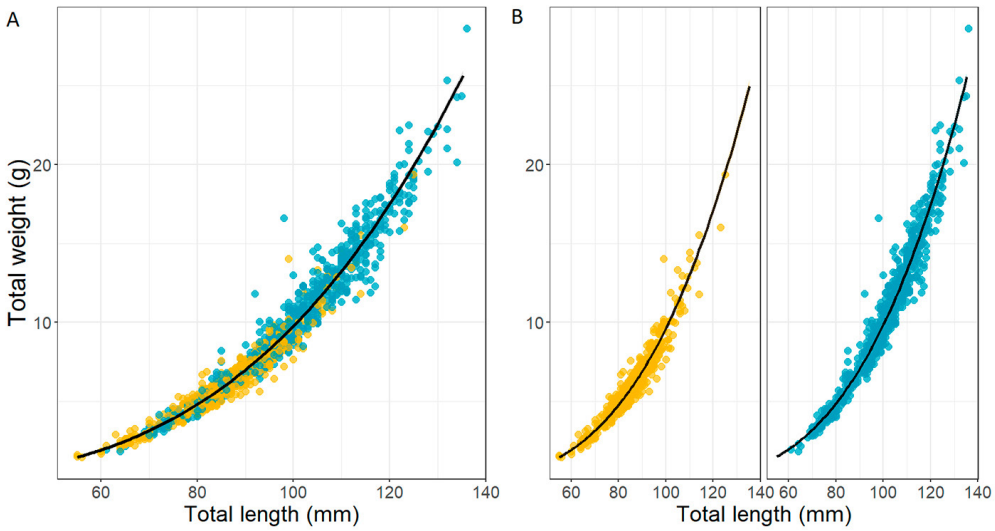

Fig. 7. – A, weight–length relationship of *B. luteum* for combined sexes. B, weight–length relationship of *B. luteum* by sex. Males and females are represented by yellow and blue, respectively. Points represent the observed data and lines the prediction from the linear regression model.

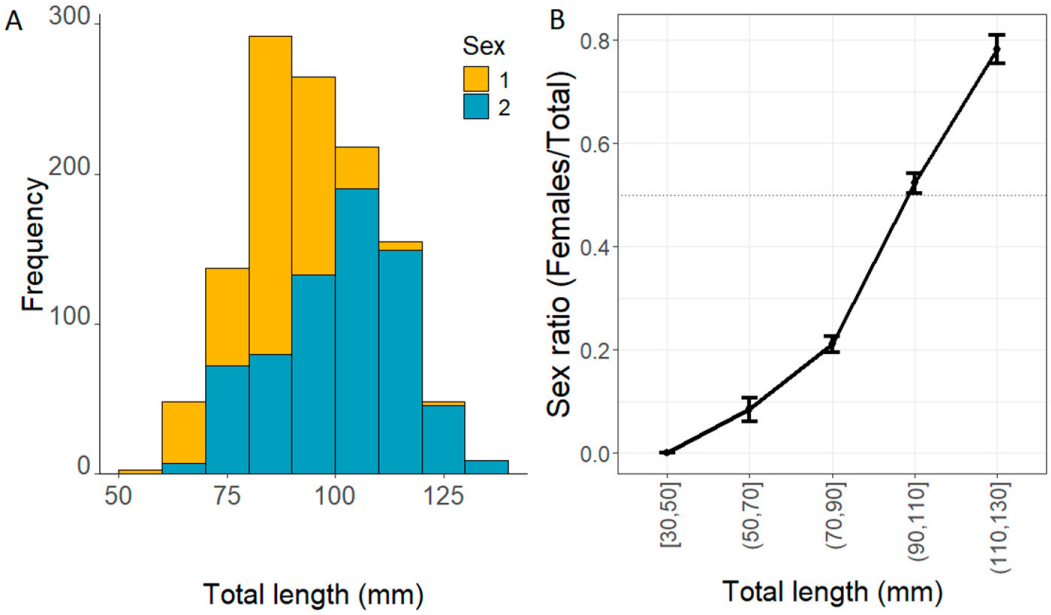

Fig. 8. – A, length frequency (in mm) for males (yellow) and females (blue) of *B. luteum*. B, sex ratio, considered as the percentage of females of the total individuals, by size intervals of 20 mm.

Maturity stages varied monthly for both sexes ($p<0.001$; Fig. 9). Developing individuals were present between March and September, whereas spawning-capable males were restricted to spring months (April and June), and females spawned from March to August. Immature and postspawning specimens occurred throughout the year. The female length at first maturity was 61 mm, with a significant size–maturity relationship ($p<0.001$; Fig. 10), with an intercept of a=–7.72 and a slope of b=0.09. The estimated L_{50} was 80.66 mm (SE 4.44 mm) and the L_{95} was 111.43 mm (SE 4.96 mm).

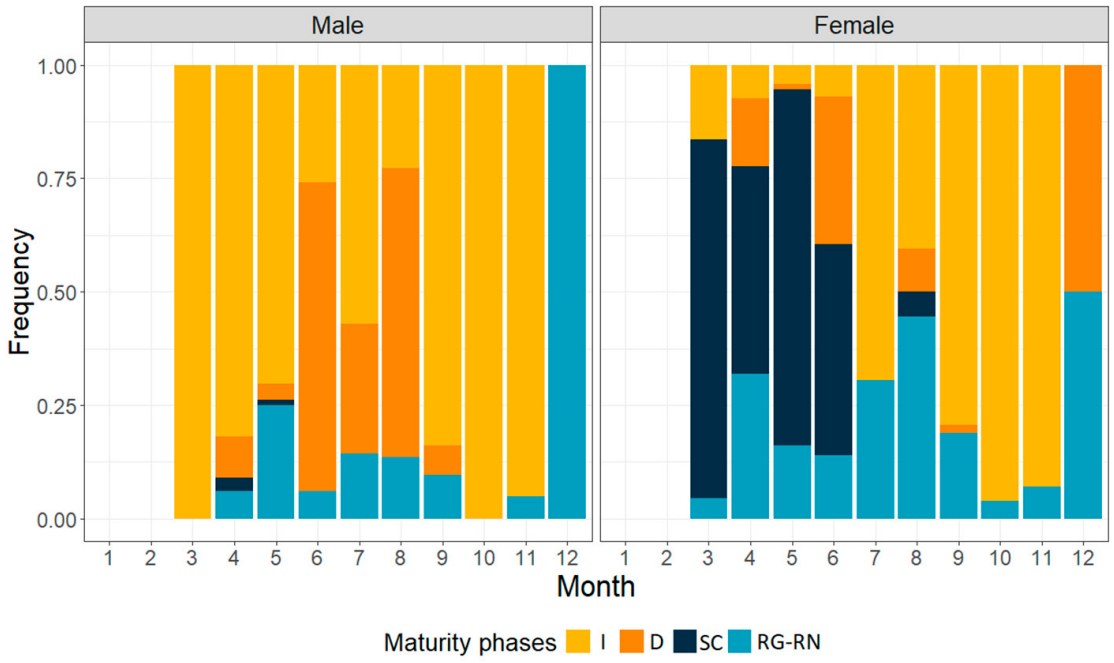

Fig. 9. – Frequency distribution (as proportion) of sexually maturity stages for males and females (based on the scale defined by the ICES WKMATCH in 2012; ICES 2014): immature (I), developing (D), spawning (SC) and regressing/regenerating (RG-RN) of *B. luteum*, captured on a monthly basis.

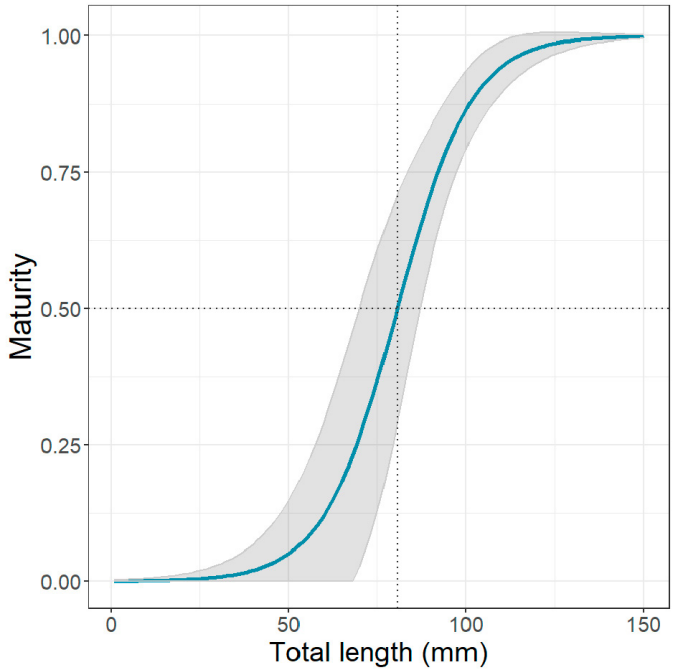

Fig. 10. – Estimated maturity ogive of *B. luteum* females. Dotted lines represent the size at 50% maturity (L_{50}=80.66 mm).

Ovaries at microscopic scale showed the same pattern as in *P. lascaris*, with a continuous development of oocytes. Actively spawning females were all in the oocyte phases, with hydrated oocytes as well as vitellogenic oocytes in different phases in the same ovary (early and late vitellogenic oocytes) (Fig. S2). Oocyte diameters ranged from 154 to 743 µm, with smaller sizes predominating. Size-frequency analysis identified three distinct modes (Fig. 11): the smallest cohort (74% of oocytes) ranged between 154 and 307 µm with a mean of 242 µm; intermediate sizes (6%) ranged between 308 and 463 µm with a mean of 373 µm; and the largest oocyte cohort (20%) ranged between 524 and 743 µm with a mean of 647 µm.

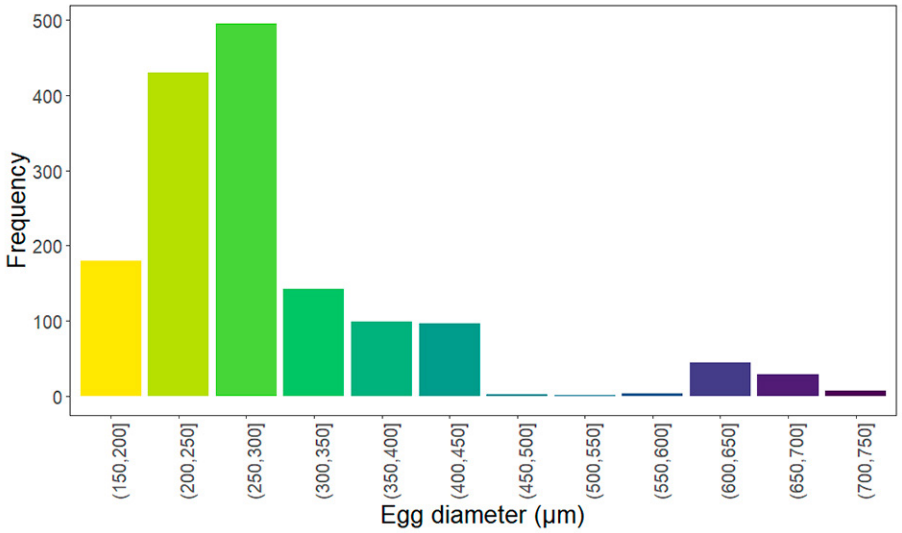

Fig. 11. – Oocyte size-frequency distribution in an actively spawning female of *B. luteum*.

DISCUSSION

Reproductive biology plays a central role in shaping the productivity of populations, directly influencing their resilience to fisheries exploitation, environmental change and anthropogenic impacts (Morgan 2008). This study provides estimates of life-history parameters of two sole species in Galician waters, *P. lascaris* and *B. luteum*.

Both species show the same growth pattern: hyperallometric growth. *P. lascaris* consistently exhibits hyperallometric growth across its distribution, with our study (b=3.14) aligning with previous studies from the Gulf of Cádiz (b=3.23; Rodríguez-García et al. 2024), Portugal (b=3.13; Mendes et al. 2004), and Mediterranean populations (b=3.43 and 3.44; Adamidou et al. 2020, Yeşilbudak 2021, respectively). The conserved positive allometry suggests strong evolutionary constraints on body shape in this species. Indeed, positive allometry is the most common pattern in fish growth (Froese 2006). Sexual dimorphism in body weight manifests through higher female weight-at-length despite similar growth coefficients between sexes (b=3.20 males, b=3.25 females), a pattern consistent with energy allocation trade-offs between growth and reproduction (Pajuelo and Lorenzo 2008).

B. luteum exhibits considerable variability in growth patterns across its distribution. While our study and others (b=3.27 in Deniel 1984; b=3.092 Pereda and Villamor 1991) report hyperallometric growth (b>3) in Atlantic populations, other regions show divergent trends: isometric growth in the Aegean Sea (b=3.01, İlkyaz et al. 2010) and negative allometry along Spain's South Atlantic coast (b=2.54, Mata et al. 2008). While in this study there were significant differences in sex, others report similar growth for males and females, such as in the Central Aegan Sea, with b=3.04 for both sexes (İlkyaz et al. 2010). The species' broad range of growth parameters suggests differences in condition between localities (Froese 2006), though hyperallometry appears dominant in most populations.

The sex ratios observed in *P. lascaris* and *B. luteum* reflect common patterns of sexual dimorphism in flatfishes, where females dominate at larger sizes—a phenomenon well-documented across multiple species (Rijnsdorp et al. 2014). In *P. lascaris*, the balanced overall sex ratio masked significant size-dependent differences, with females comprising 100% of the largest individuals. This aligns with findings of other studies in the Atlantic, which report a female-biased sex ratio in larger size classes (Deniel 1990; Pajuelo and Lorenzo 2008). Similarly, *B. luteum* exhibited pronounced female dominance (>80%) at larger sizes, consistent with reports by Nottage & Perkins (1983). This sexual size dimorphism, with males maturing younger and at smaller sizes, likely results from sex-specific energy allocation strategies (Rijnsdorp et al. 2014). Females prioritize growth to maximize fecundity (as egg production scales with body size), while males adopt a "time-minimizing" strategy, redirecting energy toward earlier maturation and shorter, more concentrated spawning periods. This trade-off between growth and reproduction is characteristic of income spawners, which rely on energy acquired during the spawning season (Rijnsdorp et al. 2014). The female-skewed sex ratio in larger size classes has important implications for fisheries management, as selective harvesting of larger individuals could disproportionately remove females, reducing the reproductive output of a population (Fenberg and Roy 2008).

Our results reveal a distinct reproductive pattern for *P. lascaris* in the study area. This pattern is characterized by the year-round presence of developing individuals, as well as a spawning period between spring and summer. For females, this period extends from May to September. For males, however, it is limited to September. It should be noted, though, that there are insufficient male samples available, possibly because they are inaccessible. This finding is similar to the prolonged spawning seasons (4–8 months) reported across most of the species' distribution (e.g. Teixeira et al. 2009, Ozyurt et al. 2018). Furthermore, the spawning season duration is related to the composition of the sand sole population because it has been observed that the spawning season is longer in older and larger fish (Pajuelo and Lorenzo 2008). However, the period of the spawning season differs depending on the region. In Portuguese waters, spawning occurs from January to June (Teixeira et al. 2009), while in the NE Mediterranean Sea, the spawning season lasts from November to June (Ozyurt et al. 2018) and on the western coast of Brittany, it lasts from May to August (Grimes 1987, Deniel et al. 1989). The species typically exhibits high fecundity during spring/summer months throughout its range. The absence of winter spawning activity in the study population, unlike the patterns documented for French and Portuguese coasts (Déniel 1981, Rijnsdorp et al. 2014), likely reflects a lack of sampling in this study during the winter season.

For *B. luteum*, our results show seasonal patterns in reproductive development. The spawning season of the species in the Ártabro Gulf occupies a protracted period, from March to August, based on the macroscopic maturity stages of females. These results generally align with previous regional studies reporting spring–summer spawning periods, though with notable geographical variation in timing. The spawning period we observed encompassed the April-July period reported by İlkyaz et al. (2010) in the Aegean Sea. However, our findings contrast with more restricted spawning periods reported in other populations at more northerly latitudes, such as March–April in the Solway Firth (Nottage and Perkins 1983) and July–August in western Ireland (Quéro et al. 1986). This geographical variability in reproductive timing likely reflects local adaptations to environmental conditions, particularly temperature regimes and productivity cycles. Indeed, differences in spawning timing across the species' spatial distribution range likely occur because it adapts its reproductive periods to ensure that larvae hatch when food availability is optimal for their survival and growth (Abookire 2006).

The estimated size at first maturity (L_{50}) is the most studied reproductive parameter of the sand sole. In our study (in the NW Spain), L_{50} was 133.64 mm, which is notably smaller than values reported in other regions. Comparative studies show considerable geographical variation: 220 mm for females in Portugal (Félix et al. 2011), 145 mm in the NE Mediterranean Sea (Ozyurt et al. 2018), 177 mm in the eastern-central Atlantic (Pajuelo and Lorenzo 2008), and 180 mm on the west coast of Brittany (Deniel 1990). Fish maturation size demonstrates considerable phenotypic plasticity (Winton et al. 2014). This regional variability in maturation size is likely to reflect differences in environmental conditions [e.g. temperature, food availability (Pauly 2021)], fishing pressure (De Roos et al. 2006,

Andersen et al. 2007) or population-specific life-history adaptations (Wilson et al. 2019). The significant differences observed highlight that maturity size is not fixed across a species' range, emphasizing the need for region-specific assessments in fisheries management and conservation strategies. In fact, such spatial variations in life-history traits must be considered when size-based fishing regulations are established (Cope and Punt 2009).

For *B. luteum*, the estimated L_{50} in our study (80.66 mm) shows noteworthy consistency with other regions: 80 mm in the Bay of Biscay (Félix et al. 2011) and 81 mm in the Aegean Sea (İlkyaz et al. 2010). This unusual stability in maturation size across the species' distribution may reflect the relatively low fishing pressure on *B. luteum* compared with commercially important species (Hixon et al. 2014). Unlike heavily exploited species that often show fishing-induced evolution of life-history traits (e.g. reduced L_{50} under high exploitation) (Heino et al. 2015), the absence of strong fisheries selection in this by-catch species may have allowed it to maintain its natural maturation process (Law 2000).

Taken together, the results indicate that the two sole species in our study share similar reproductive features typical of batch spawners with asynchronous oocyte development and indeterminate fecundity. This is evidenced by (1) the simultaneous presence of oocytes at all developmental phases without dominant populations (Murua et al. 2003), and (2) the co-occurrence of postovulatory follicles with advanced vitellogenic oocytes, indicating multiple spawning events (e.g. in *P. lascaris* it was observed that spawning takes place in two or three batches; Deniel et al. 1989, Pajuelo and Lorenzo 2008). These features align with the general reproductive pattern observed in most flatfish species (Rijnsdorp et al. 2014). The asynchronous ovarian development results in a multimodal oocyte size-frequency distribution, with overlapping cohorts visible throughout the reproductive season (Tyler and Sumpter 1996). Only during final maturation does a clear separation appear between hydrated oocytes and other developmental phases (Hunter et al. 1985). This strategy allows continuous oocyte recruitment and batch spawning over an extended period (Stark 2004), as observed in our study, where spawning-capable females in both species were present for several months. The non-synchronous initiation of vitellogenesis among females was already observed by Pajuelo and Lorenzo (in 2008) for *P. lascaris*. The year-round presence of immature and postspawning specimens in our study further supports the asynchronous development pattern common in flatfishes with prolonged reproductive seasons (McEvoy 1984, Nagler et al. 1999).

The indeterminate spawning strategy provides ecological advantages by increasing offspring survival probability through temporal spreading of reproductive effort (Lambert and Ware 1984, Rijnsdorp et al. 2014), allowing flexible responses to environmental fluctuations and enabling energy allocation to reproduction as resources become available (Hunter and Leong 1981). In fact, this reproductive plasticity likely enhances population resilience (Rijnsdorp et al. 2014).

Therefore, the findings of this study highlight the reproductive strategy of these two species in the Ártabro Gulf. The study also highlights the importance of continued research to obtain more robust results, particularly for reproductive studies. The future steps include increasing the number of samplings, as well as more gonad data to enhance the reliability of the data, which will be crucial for the sustainable management and conservation of these two sole species.

SUPPLEMENTARY MATERIAL

The following supplementary material is available through the online version of this article:

Fig. S1. – Microscopic maturity phases of *P. lascaris* females (based on the scale defined by Brown-Peterson et al. 2011).

Fig. S2. – Microscopic maturity phases of *B. luteum* females (based on the scale defined by Brown-Peterson et al. 2011).

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DECLARATION OF COMPETING INTERESTS

The authors of this article declare that they have no financial, professional or personal conflicts of interest that could have inappropriately influenced this work.

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AUTHORSHIP CONTRIBUTION STATEMENT

Cristina García-Fernández: Conceptualization, Data curation, Formal analysis, Investigation, Writing – original draft, Writing – review & editing. **Patricia Verísimo:** Investigation, Writing – review & editing. **Helena Regueiro:** Investigation, Methodology, Writing – review. **Dolores Garabana:** Conceptualization, Investigation, Methodology, Writing – review & editing. **Paz Sampedro:** Funding acquisition, Project administration, Investigation, Supervision, Writing – review & editing.

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