

Reproductive traits exhibited by the paedomorphic gobies exploited in the Majorcan transparent goby fishery (western Mediterranean) and their management implications

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Summary: An important small-scale fishery in Majorca targets three similar goby species: *Aphia minuta*, *Pseudaphia ferreri* and *Crystallogobius linearis*. Histological examination of the gonads of these species sampled from landings during the fishing season revealed characteristic reproductive traits that could be defined as abbreviate iteroparity. The transparent goby (*Aphia minuta*) and Ferrer's goby (*Pseudaphia ferreri*) showed batch abbreviate iteroparity as a reproductive strategy, whereas the crystal goby (*Crystallogobius linearis*) showed total abbreviate iteroparity. Despite their short lifespans, all of them have a spawning season whose duration is longer than the legal fishing season. Additionally, all of them maintain a standing stock of primary growth oocytes in their gonads, indicating more than one spawning season in their lifespan. These reproductive features partially offset their special sensitivity to potential overexploitation and environmental changes but also suggest that the fishery needs special management to avoid breaking the balance between sustainability and fishing effort. The results of size at maturity and potential annual fecundity in the three species of the fishery are also reported and discussed.

Keywords: *Aphia minuta*; *Pseudaphia ferreri*; *Crystallogobius linearis*; reproduction; abbreviate iteroparity; batch spawners; histology.

Rasgos reproductivos de los gobios paedomórficos explotados en la pesquería del jonquillo de Mallorca (Mediterráneo occidental) y sus implicaciones en la gestión.

Resumen: En Mallorca existe una importante pesquería artesanal basada en la captura de 3 especies de gobios similares (*Aphia minuta*, *Pseudaphia ferreri* y *Crystallogobius linearis*). El examen histológico de las gónadas de muestras obtenidas de los desembarques realizados durante la temporada de pesca reveló rasgos reproductivos característicos que podrían definirse como iteroparidad abreviada. El chanquete o jonquillo (*Aphia minuta*) y el cabotí (*Pseudaphia ferreri*) mostraron una estrategia reproductiva de iteroparidad abreviada múltiple, mientras que el gobio de cristal (*Crystallogobius linearis*) mostró iteroparidad abreviada total. A pesar de su corta esperanza de vida, todos ellos tienen una larga época de puesta, cuya duración es mayor que la temporada de pesca autorizada. Además, todos ellos mantienen una reserva permanente de ovocitos de crecimiento primario en sus gónadas, lo que indica más de un período de puesta a lo largo de su vida. Estas características reproductivas compensan en parte su especial sensibilidad a posibles sobreexplotaciones y cambios ambientales, pero al mismo tiempo implican la necesidad de una gestión especial de la pesquería para evitar romper el equilibrio entre sostenibilidad y esfuerzo pesquero. También se reportan y discuten los resultados de talla de madurez y fecundidad anual potencial en las tres especies de la pesquería.

Palabras clave: *Aphia minuta*; *Pseudaphia ferreri*; *Crystallogobius linearis*; reproducción; iteroparidad abreviada; reproductor múltiple; histología.

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INTRODUCTION

The transparent goby fishery is a traditional, seasonal small-scale fishery, in which a boat-seine net (known as the *jonquillera* in the Balearic Islands) is hauled over the bottom in winter, between depths of 5 and 40 m (Iglesias and Martorell 1992). Small annual progenetic gobies are the target species of this fishery, which specifically operates in the western and central Mediterranean off the coasts of Spain and Italy. Fisheries operations take place during one fishing season each year, generally from November to April, in concomitance with the coastal migration and shoaling behaviour of juveniles in winter (Iglesias and Morales-Nin 2001, La Mesa et al. 2005). This century-old seasonal fishery is of great socioeconomic importance in the Mediterranean, commanding high market prices (from €20 to €40 per kg; Morales-Nin et al. 2017). However, in all the localities where the transparent goby fishery is exploited, the annual catch differs considerably across fishing seasons (Iglesias and Morales-Nin 2001) because these fisheries are based on catches of annual species depending primarily on the success of recruitment from the previous spawning season, which is, in turn, environmentally dependent (Santojanni et al. 2006). Additionally, the fishing activity during key life-history periods may also have negative effects (Tzanatos et al. 2005), even leading to the collapse and disappearance of the fishery, as in the Bay of Malaga (La Mesa et al. 2005) or taking it dangerously close to collapse, as happened in the Mallorca fishery in the 1990s (Iglesias and Morales-Nin 2001).

Due to its particular characteristics (secular tradition and stock fragility), the transparent goby fishery is considered a “special fishery” by the Commission of the European Communities (2004), which means that the fishing activities are managed locally in derogation from the general European rules. These “special fisheries” are permitted in restricted areas in which the resource is particularly abundant and traditionally exploited (La Mesa et al. 2005). This is the case for the small gobies population on Mallorca Island, which experienced some recovery in the early 2000s (Morales-Nin et al. 2022). Consequently, and owing to a special exemption from the European Union (initially by Commission Execution Regulation (EU) 1233/2013, of November 29 and currently by Commission Execution Regulation (EU) 2020/1243, of September 1, 2020), the fishery in the Balearic Islands has been regulated since 2013 through management plans (initially by Decree 46/2013, of October 4, and currently by Decree 31/2021, of May 31) of the Autonomous Government of the Balearic Islands, in which the fishing agents participate in a co-management committee (Morales-Nin et al. 2017). Co-

management is conceived as an ongoing collaborative and communicative process that continues to evolve over time. In this plan, only boats based at seven harbours off Mallorca Island can be registered for the fishery. The peculiar life cycle of the target species and the dependence of the fishery on seasonal recruitment mean that it cannot use current population evaluation methods, and stakeholders must focus on maintaining sustainability in their practices (Morales-Nin et al. 2022). Specifically, fishery regulation is based on temporary revised measures: daily quota, specific licences, equipment control and seasonal closure, among others (Morales-Nin et al. 2017).

The main target species of this fishery throughout the Mediterranean is the transparent goby, *Aphia minuta* (Risso 1810), but at Mallorca Island there is a second target species, Ferrer’s goby, *Pseudaphya ferreri* (De Buen and Fage 1908). Interestingly, higher prices are achieved depending on the proportion of *A. minuta* in the landing (Morales-Nin et al. 2017). Additionally, the crystal goby, *Crystallogobius linearis* (Düben 1845), is another small goby considered a bycatch but with special interest because it is sold with the target species, so it has commercial value. The three species share morphological and evolutive traits (Kon and Yoshino 2002); they are small, progenetic pelagic species (<60 mm total length, L_T) that do not live more than one year (De Buen 1931). In previous studies conducted on *A. minuta* in waters off Majorca, the oldest individuals were 7-8 months old (Iglesias et al. 1997). All these species have similar life-history strategies, generally showing a short lifespan, a rapid achievement of sexual maturity, planktotrophic habits and, often, sudden death of breeders soon after spawning. In addition, these species are characterized by the persistence of ecological and anatomical postlarval features into their adulthood (Miller 1973) as a significant adaptation for a planktotrophic life in midwater (Brunelli and Atella 1914). Hence, they retain some postlarval traits, such as body transparency and the scarcity of melanophores, the persistence of the swim bladder and a short and virtually straight alimentary canal. The retention of larval morphology in adults, or paedomorphosis, is achieved through heterochrony, consisting of a change in the timing and/or rates of processes underlying the ontogenic formation of morphological traits compared with the ancestral species (Gould 1977).

To guarantee the sustainability of the fishery, knowledge of the reproductive biology of these species is essential for fisheries management. However, the estimations of their sexual maturity are usually based on macroscopic observations of the gonads, but these are inherently error-prone because gametocytes of small size can be present in the gonads but are not eye

visible, and immature oocytes may be hidden by those in a more advanced stage of development (Caputo et al. 2000, Lowerre-Barbieri et al. 2011b). Accordingly, many macroscopic-based reproductive studies have been carried out in *Aphia minuta* throughout the Mediterranean: from December to April and from June to November in the coastal waters off Majorca (Iglesias and Morales-Nin 2001); from January to March in Murcia (southeastern coast of Spain, Martínez-Baño et al. 1993); from February to March and September in the Ligurian Sea (Relini et al. 1998); from March to September in the Tyrrhenian Sea (Baino et al. 1996, Auteri et al. 2000); and at least 6 months (from April to September) in the central Adriatic Sea (Mancini and Cavinato 1969, La Mesa 1999, Caputo et al. 2000). These studies have shown surprising and somewhat contradictory seasonal spawning differences.

Regarding their reproductive strategies, *A. minuta* had been traditionally considered semelparous (Miller 1989), with a single reproductive event followed by death. However, Caputo et al. (2000) demonstrated that the species is in fact an abbreviate iteroparous breeder, with more than one spawning season in its short lifetime. A disparity of criteria have also been observed in its potential annual fecundity, ranging between 900 and 7000 oocytes per female (Iglesias and Morales-Nin 2001, Frogliola and Grammito 1989, Auteri et al. 2000).

The reproductive information available on *P. ferreri* and *C. linearis* is more limited. *P. ferreri* is distributed in the western Mediterranean and Adriatic Sea, and its reproductive features are poorly understood (La Mesa 2011). Fage (1910) suggested that the breeding season of this species occurs in June on the basis of a ripe female of 35 mm caught off Cap d'Ail (Monaco). Size at maturity is approximately 26 to 27 mm L_T (Miller 1973). Related to the crystal goby, it is distributed in the eastern Atlantic, from Norway to Gibraltar, and it is also known from the Mediterranean Sea and Madeira Islands. *C. linearis* is generally considered a single spawner (i.e. semelparous sensu Cole 1954), with a single breeding season between March/August and July/September in North Atlantic and Mediterranean waters, respectively (Collet 1878, Padoa 1956). Accordingly, Caputo et al. (2003) pointed out that the crystal goby is a truly semelparous species, since the mature gonads of both males and females appeared to have lost their recruitment capability after their first spawning.

Since reproductive traits are highly plastic and quite variable depending on the environmental characteristics

and fishing pressure (Lowerre-Barbieri et al. 2011b), a complete gonad histological study of *A. minuta*, *P. ferreri* and *C. linearis* was conducted from landings of the commercial small-scale fishery off Majorca Island. The specific objectives were to study the reproductive cycle of the three species, their reproductive strategies and fecundity ranges, and their size at maturation, in order to help stakeholders refine management measures according to reliable reproductive data.

MATERIALS AND METHODS

Sampling and histological processing

A total of 627 wild fish were collected from landings of the commercial small-scale fishery in the five main ports around Mallorca (Fig. 1). Sampling spanned one whole authorized fishing season from December 2015 to April 2016. Sampling did not span the entire year because fishing is forbidden during closed seasons (Decree No 46/2013 and Decree No 31/2021). As far as possible, a minimum number of 30 specimens per species per month were randomly sampled. The 627 sampled specimens were distributed as follows: 255 were *A. minuta*, 240 were *P. ferreri* and 132 were *C. linearis* (Table 1). Somatic weight (Ws) was determined from fresh to the nearest 0.0001 g, and L_T was determined to the nearest 0.001 mm with an electronic profile projector (Mitutoyo, Model PJ-A3000, Japan). Afterwards, whole individuals were preserved in 10% phosphate-buffered formalin for at least one week.

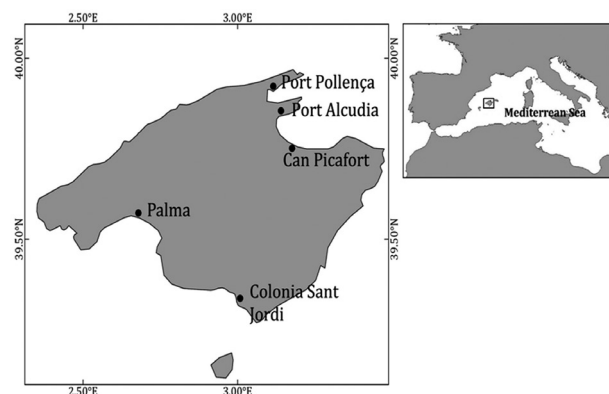


Fig. 1. – Sampled ports of the transparent goby fishery of Mallorca Island (western Mediterranean).

Table 1. – Number of specimens sampled during the fishing season 2015-2016 and the total length range (L_T range) in mm, the total length mean (L_T mean) in mm and the standard error (sd) in mm, by species and month.

	N						L_T range	L_T mean \pm sd
	Dec. 2015	Jan. 2016	Feb. 2016	Mar. 2016	Apr. 2016	Total		
<i>Aphia minuta</i>	80	70	45	30	30	255	18.760-40.686	33.862 \pm 4.044
<i>Pseudaphia ferreri</i>	75	45	60	45	30	240	15.035-31.909	24.847 \pm 3.687
<i>Crystallogobius linearis</i>		42	30	30	30	132	17.143-38.290	26.829 \pm 4.063

The study was conducted by species and the study of gonad development was based on microscopic observations performed with an Olympus BX51 microscope. Because of the very small size of the gonads (which involves an inherent difficulty in dissecting them without gonad damage), two transversal portions of the whole fixed fish, cut at the abdominal level, were histologically processed. These abdominal sections of the fish were embedded in Paraplast Plus (Kendall), sectioned at 3 to 4 μm and stained with Mayer's haematoxylin and eosin for routine microscopic examination (Luna 1968).

The gonads were histologically sexed and classified into four maturity stages according to the terminology reported by Brown-Peterson et al. (2011) (Table 2). The terminology employed by Grau et al. (1996 and 2009) was used in histological oocyte staging. Ovary maturity stages were based on the most advanced oocytes and the occurrence of postovulatory follicles. Male gonad stages were based on male germ cell development and the presence of spermatozoa in the lumen of lobules and in the vas deferens.

Reproductive cycle, sex ratio and size at maturation

Histological determinations were used to establish sex, gonad development, spawning period, reproductive strategy, reproductive cycle and size at maturation. Specimens were pooled by month for the different analyses. Females were considered mature from stage F2 to F4, and males were considered mature from stage M2 to M4 (Table 2). The reproductive cycle was determined according to the observed maturity stages, and it was compared with previous results obtained from the same fishery and from the same area by other authors (Iglesias et al. 1997, Iglesias and Morales-Nin 2001).

Chi-square (χ^2) analysis was used to test whether the sex ratio by month deviated from 1:1.

Female and male length at 50% maturity (L_{50}) was estimated from the maturity ogive during the fishing season. The proportion of mature specimens was pooled into 1 mm length intervals and fitted to this logistic equation:

$$P=1/(1+e^{a+b*LT})$$

where P is the probability of being mature, a and b are constants, and L_T is the independent variable described by Sparre and Venema (1992).

A total of 344 fish were analysed for this purpose: 97 females (18.760-39.505 mm, L_T) and 45 males (25.816-40.686 mm, L_T) of *A. minuta*; 121 females (15.392-31.909 mm, L_T) and 46 males (15.569-29.911 mm, L_T) of *P. ferreri*; and 35 males (20.954-38.29 mm, L_T) of *C. linearis*. L_{50} was not determined in females of *C. linearis* owing to the lack of immature females in the observed samples, which made it impossible to estimate L_{50} .

To estimate the age at 50% maturity (A_{50}) in *Aphia minuta*, Von Bertalanffy growth parameters published for the species from the same fishery (Iglesias et al. 1997) were compared with length data obtained in the current study.

Ovarian development organization, spawning pattern and fecundity

The classifications defined by Marza (1938) and Wallace and Selman (1981), by Tyler and Sumpter (1996) and by Hunter et al. (1992) were used to determine, respectively, the ovarian development organization, the spawning pattern and the type of fecundity (in Murua et al. 2003). For this purpose, histological sections and oocyte size-frequency distributions were analysed. The latter were performed, following West (1990), from measurements of a minimum of 100 oocytes of 10 mature females per species, fished just before the spawning activity peak. Measurements were performed with Analysis-get IT software connected to an Olympus-SZH stereomicroscope.

Owing to the extremely short lifetime of the species (less than one year; De Buen 1931) and the abbreviate iteroparous character of the three species (Caputo et al 2000; see results), which can be assimilated in annual terms to semelparity for fecundity estimation purposes, the potential annual fecundity (F_p) was estimated. F_p was defined as the number of oocytes per female

Table 2. – General histological description of developmental gonad stages for females and males of *A. minuta*, *P. ferreri* and *C. linearis*.

Stage (or Phase)	FEMALE
I Immature	Small ovarian cavity. Lamellae containing numerous oogonia, chromatin-nucleolus stage and perinuclear oocytes
II Early developing	Numerous primary growth oocytes, together with secondary oocytes at the cortical alveolus stage
III Late developing	Wide ovarian cavity with batches of primary growth, cortical alveolus and vitellogenic oocytes
IV Spawning capable	Wide ovarian cavity with batches of secondary growth oocytes at Germinal vesicle migration, hydrated oocytes and postovulatory follicles
MALE	
I Immature	Very small gonad. Abundant spermatogonia and spermatocytes
II Early developing	Most of the cells are spermatocytes and spermatids.
III Late developing (ripe)	In addition to the spermatocytes and spermatids, spermatozoa can be observed at this stage.
IV Spawning capable (running)	Intense spermatogenic activity. Dilated tubules and vas deferens. Plenty of spermatozoa are observed.

uncorrected for atretic losses and was estimated by a gravimetric method. However, the small size of the individuals (and, therefore, of their gonads) entails that it is impossible to determine fecundity and maturity gonad stage in the same specimen. Therefore, to ensure the use of only mature females just prior to spawning for fecundity determination, mature females with an L_t over the L_{50} and fished just before the spawning peak were selected. Following these requirements, 52 fixed mature females of *A. minuta* (30.802-41.785 mm L_t in fresh), 10 fixed mature females of *P. ferreri* (27.915-32.231 mm L_t in fresh) and 10 fixed mature females of *C. linearis* (24.364-30.561 mm L_t in fresh), caught prior to the spawning peak (between January and March, see results), were chosen, and the gonads were removed and weighed to the nearest 0.0001 mg. A portion of 0.01 g from each gonad (approximately 20% of the total gonad weight) was extracted and dissected, and all the observed oocytes were counted using Analysis-get IT software connected to an Olympus-SC30 video camera under an Olympus-SZH stereomicroscope. In the case of *C. linearis*, as the gonad size and the number of oocytes were smaller than those in *A. minuta* and *C. linearis*, the whole gonad was disaggregated and counted.

The relationship between fecundity and somatic (L_t , W_s) variables was analysed by simple regression analysis in *A. minuta*. The predictors and dependent variables were log-transformed to achieve normality and homogeneity of variances. In *P. ferreri* and *C. linearis*, the relationships were not tested because the number of counts was not sufficient to achieve significant results.

RESULTS

Aphia minuta

Length structure of the sampled population and sex ratio

The sampled *Aphia minuta* ranged between 18.760 and 40.686 mm L_t (Table 1, Fig. 2A), showing

the mean L_t increasing by month throughout the fishing season (Table 3); for all months, males were significantly larger than females ($F=11.116$, $p=0.001$; Fig. 3A, Table 3). The L_t maximum size was 40.686 mm in males and 33.179 mm in females (Table 3). The number of sexually undetermined fish decreased with length (Fig. 2A).

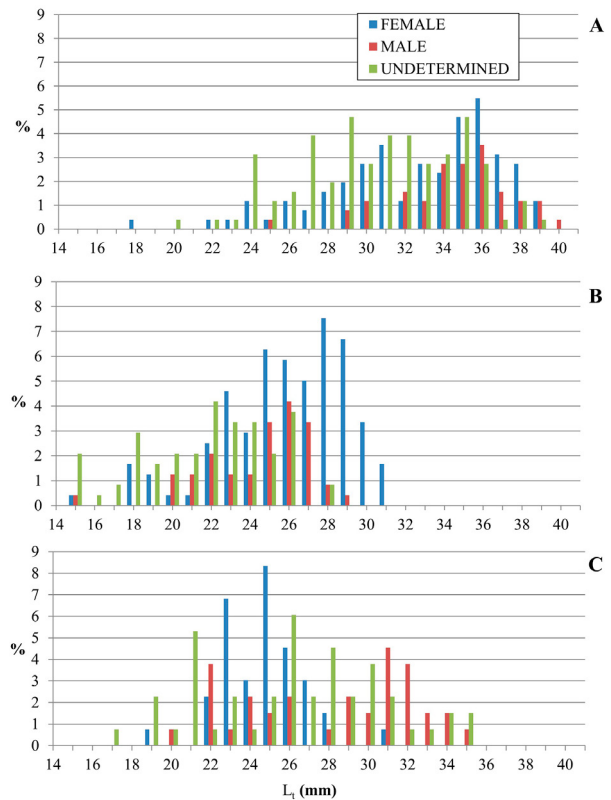


Fig. 2. – Length-frequency distributions for females (blue bars), males (red bars) and undetermined (green bars) of *Aphia minuta* (A), *Pseudaphia ferreri* (B) and *Crystallogobius linearis* (C). Data grouped by 1 mm L_t .

Table 3. – Total length range (L_t range), total mean length (L_t mean) and standard error (sd) in mm of males, females and both of *Aphia minuta* throughout the fishing season.

Month	Females			Males			Both		
	N	L_t range (mm)	L_t mean \pm sd (mm)	N	L_t range (mm)	L_t mean \pm sd (mm)	N	L_t range (mm)	L_t mean \pm sd (mm)
Dec. 2015	24	18.760-33.283	28.667 \pm 3.616	9	25.816 - 33.630	30.802 \pm 2.441	33	18.760-33.630	29.249 \pm 3.438
Jan. 2016	26	24.238-36.622	31.742 \pm 3.455	8	30.945 - 36.447	34.136 \pm 1.770	34	24.238-36.622	32.305 \pm 3.282
Feb. 2016	18	30.964-39.505	36.086 \pm 2.748	13	34.807-40.686	37.328 \pm 1.980	31	30.964-40.686	36.607 \pm 2.497
Mar. 2016	16	33.377-38.499	36.527 \pm 1.288	10	33.910-38.342	36.057 \pm 1.348	26	33.377-38.499	36.346 \pm 1.306
Apr. 2016	13	32.792-39.026	36.816 \pm 1.548	7	34.173-38.611	36.308 \pm 1.462	20	32.792-39.026	36.639 \pm 1.500
Total	97	18.760-39.026	33.256 \pm 4.362	47	25.816-40.686	35.112 \pm 2.961	144	18.760-40.686	33.862 \pm 4.044

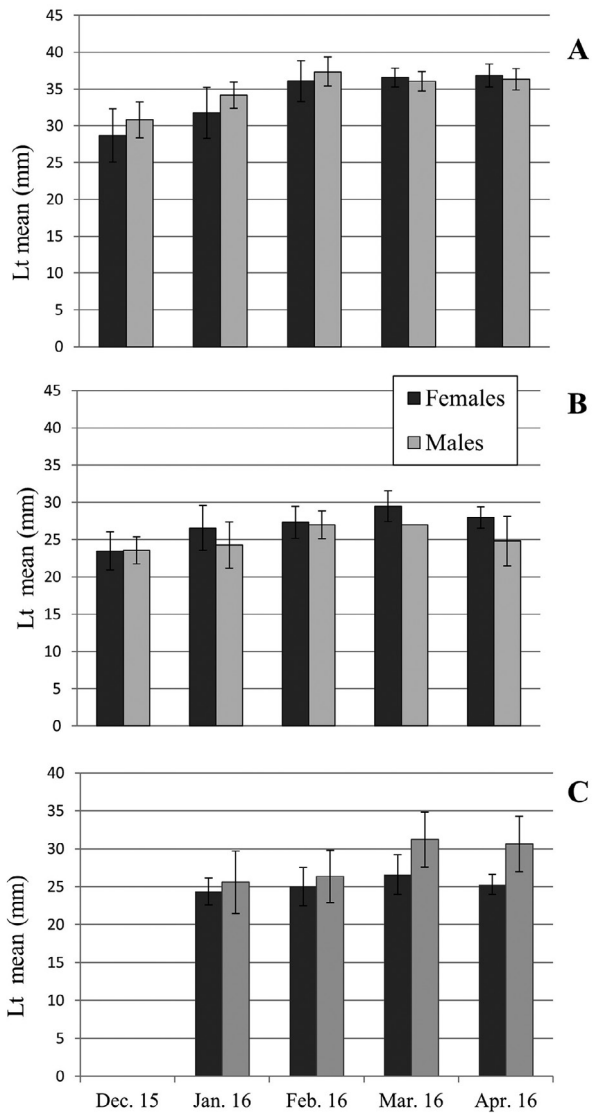


Fig. 3. – Mean total length (L_t in mm, by month and by sex, throughout the fishing season 2015-2016) in sampled *Aphia minuta* (A), *Pseudaphia ferreri* (B) and *Crystallogobius linearis* (C). The bars represent the standard deviation.

Of the 255 fish analysed, the sex was determined in 144 specimens (56.5%), 97 females and 47 males, but was not determined in 111 individuals. The overall sex ratio was significantly skewed to females (2.06 females/males, $p < 0.05$). When the sex ratio was analysed per month, all the results were skewed to females (Table 4), but no significant differences were observed in February, March and April.

Seasonal trends in gonad development, reproductive strategy and size at maturation

The monthly evolution of the ovary maturity stages indicates that the reproductive cycle is asynchronous at the population level (i.e. not all the individuals were at the same gonad development stage at the same time) (Fig. 4A). Females in the early developing stage (or phase) were observed from December onwards in all

Table 4. – Sex ratio throughout the spawning season of *A. minuta*, *P. ferreri* and *C. linearis*. * $p < 0.05$.

Month	<i>A. minuta</i>		<i>P. ferreri</i>		<i>C. linearis</i>	
	N	M:F	N	M:F	N	M:F
Dec. 2015	33	1:2.67*	49	1:3.45*	0	
Jan. 2016	34	1:3.25*	44	1:1.75	20	1:1.22
Feb. 2016	31	1:1.38	34	1:1.43	18	1:1.25
Mar. 2016	26	1:1.6	21	1:2.0*	21	1:0.4
Apr. 2016	20	1:1.86	20	1:3*	19	1:2.8*
Fishing season 2015-16	144	1:2.06*	168	1:2.57*	78	1:1.11

the sampled months. The spawning capable phase was first observed in January and peaked in March, with 75% of females actively spawning (Fig. 4A, Table 5). When sampling finished for legal reasons, 69.23% of females were still at the spawning capable stage. Running males (Fig. 5B) were found from February to April, with a peak in April (28.57%) (Fig. 4B, Table 5), and were also actively spawning at the end of the sampling period. Immature females were observed from December to February, while immature males were observed in all the sampled months. The percentages of immature specimens decreased progressively in general in both sexes during the sampling period (Fig. 4A, B, Table 5). Postspawning individuals were not observed.

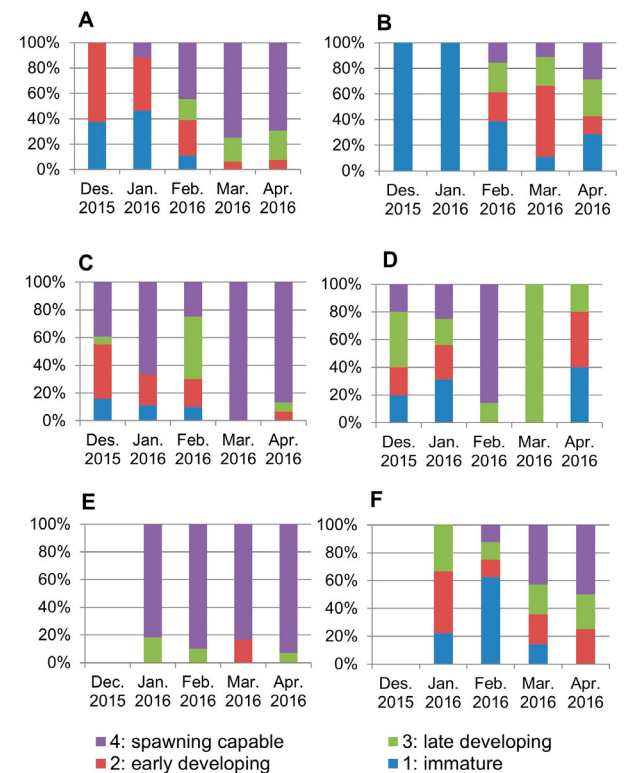


Fig. 4. – Monthly evolution of gonad stages of *Aphia minuta* (A, female; B, male), *Pseudaphia ferreri* (C, female; D, male) and *Crystallogobius linearis* (E, female; F, male), during the 2015-2016 fishing season.

Table 5. Percentage of spawning capable specimens (%) with respect to the total number per month (N) by species and sex throughout the 2015-2016 fishing season.

	<i>Aphia minuta</i>				<i>Pseudaphia ferreri</i>				<i>Crystallogobius linearis</i>			
	Males		Females		Males		Females		Males		Females	
	N	%	N	%	N	%	N	%	N	%	N	%
Des. 2015	9	0	24	0	11	20	38	39.47	0	-	0	-
Jan. 2016	8	0	26	11.54	16	25	28	66.67	9	0	11	81.82
Feb. 2016	13	15.38	18	44.44	14	85.71	20	25	8	12.5	10	90
Mar. 2016	10	11.11	16	75	1	0	20	100	15	42.86	6	83.33
Apr. 2016	7	28.57	13	69.23	5	0	15	86.67	5	50	14	92.86

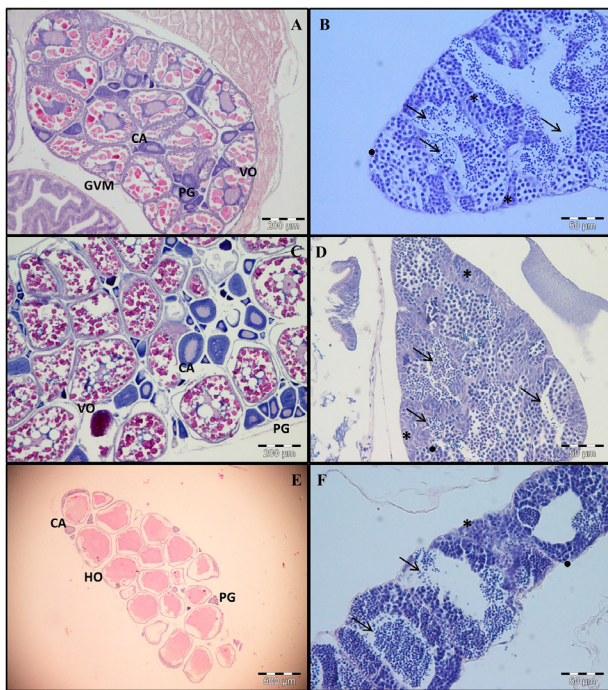


Fig. 5. – Histological sections of spawning capable specimens (stage IV) of *Aphia minuta* (A, female; B, male), *Pseudaphia ferreri* (C, female; D, male) and *Crystallogobius linearis* (E, female; F, male). Spawning capable females of *A. minuta* and *P. ferreri* (A, C): secondary growth oocytes at the cortical alveolus stage (CA), vitellogenic oocytes (VO) and germinal vesicle migration (GVM) are observed together with primary growth oocytes (PG); in *C. linearis* (E), gonads are fully filled with hydrated oocytes (HO), and few primary growth oocytes are observed. Spawning capable males (B, D, F): tubules and vas deferens are full of spermatozoa (♂); in addition, spermatocytes (*) and spermatids (•) can be observed.

Microscopic observations of the ovaries of *Aphia minuta* in spawning capable females revealed at least two populations of oocytes: a relatively synchronous larger population of vitellogenic oocytes (or batch) and a more heterogeneous population of smaller ones, including primary growth (PG) oocytes (Fig. 5A). The ovarian oocyte size-frequency distribution of *Aphia minuta* ranged between 20 and 860 μm , showing a trimodal ovarian organization with three batches (or groups) of oocytes separated by two large hiatuses, ranging between 260–400 μm and 620–680 μm in size (Fig. 6A). The development of the first large hiatus separating the stock of vitellogenic oocytes from the heterogeneous population of smaller ones in the oocyte

size-frequency distribution indicates that fecundity is determinate. Furthermore, the species is a batch spawner, wherein all the oocytes to be spawned in a season are recruited to secondary growth in different batches prior to the first spawning event, as indicated by the separate modes observed in recruitment (Fig. 6A) and corroborated by the presence of postovulatory follicles in spawning capable females. Additionally, *Aphia minuta* females also maintain an important reserve of PG oocytes in their ovaries (Fig. 5A) that would be recruited in a future spawning event, indicating iteroparity.

With respect to size at maturation, the smallest mature female was 24.164 mm L_T , and size at 50%

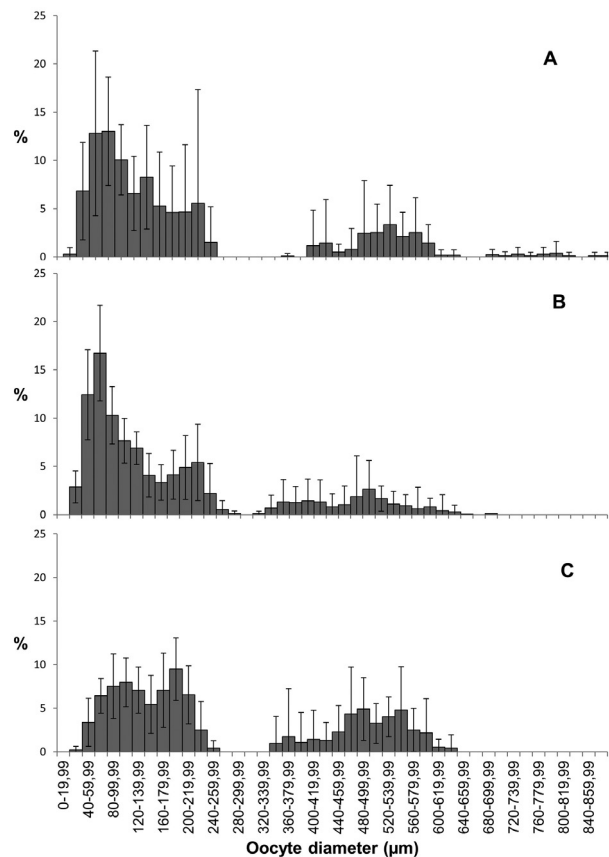


Fig. 6. – Mean size-frequency distribution of oocyte diameters, grouped per 20 μm , from histological sections in females of *Aphia minuta* (A), *P. ferreri* (B) and *C. linearis* (C) sampled in February before the spawning peak. Bars indicate standard error.

maturity of females was estimated to be 28.457 mm L_T (logistic Model 95% CI=26.263-30.650 mm, Fig. 7A). In the case of males, the smallest mature specimen was 33.910 mm L_T . The size at 50% maturity of males was estimated to be 35.116 mm L_T (logistic Model 95% CI=34.260-35.972 mm, Fig. 7A). We estimated A_{50} at 199 days per male and 105 days per female, adjusting our data to the published Von Bertalanffy growth equation (Iglesias et al. 1997). According to our data, A_{max} was estimated at 230 days.

Fecundity

Due to technical limitations of the dissection, Fp was estimated in 47 of the 52 initially selected ovaries

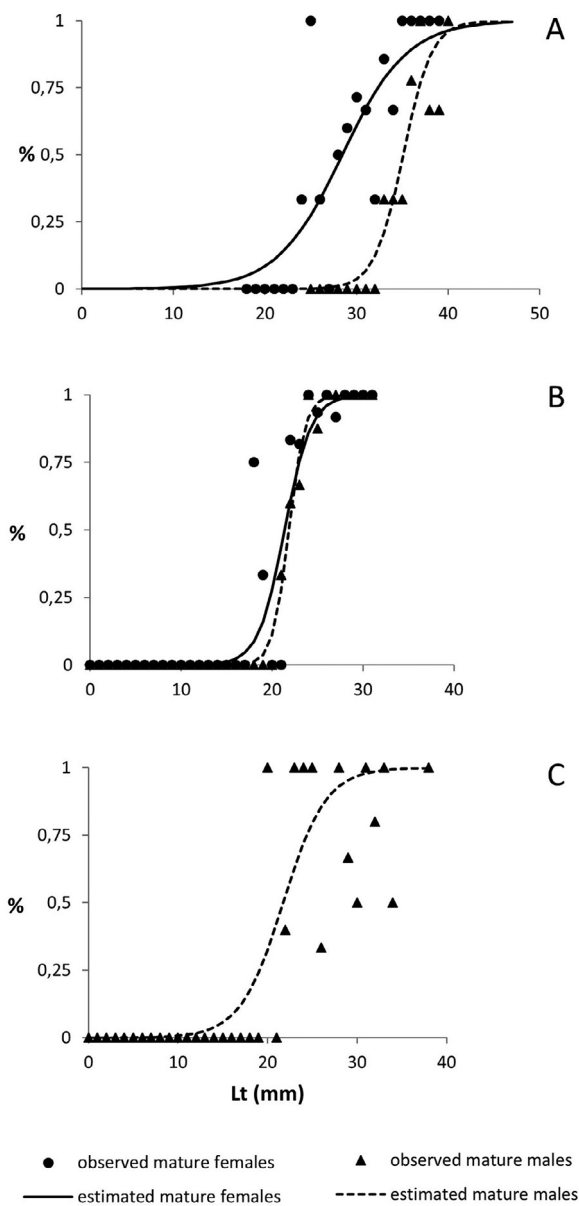


Fig. 7. – Percentage of mature females and males per length class of *Aphia minuta* (A), *Pseudaphia ferreri* (B) and *Crystallogobius linearis* (C). Solid lines indicate estimates of size and age at 50% maturity in females, and dashed lines indicate estimates of size and age at 50% maturity in males.

(corresponding to females ranging from 30.802 to 41.785 mm L_T). The Fp ranged between 1746 (in a female of 33.082 mm, L_T) and 6600 oocytes (in a female of 40.917 mm L_T), with an average of 3609.87 ± 1134.42 sd. The oocyte diameter ranged between 0.020-0.880 μ m. The number of oocytes in females of similar length and weight varied greatly, as shown by the low r^2 (L_T $r^2=0.045$ and W_s $r^2=0.032$).

Pseudaphia ferreri

Length structure of the sampled population and sex ratio

The L_T of the sampled *Pseudaphia ferreri* ranged between 15.035 and 31.909 mm (Table 1, Fig. 2B). The mean sizes increased from December to March, and considering all the months, significant differences between the L_T of females and males were not detected ($F=1.124$, $p=0.291$, Fig. 3B). The maximum size observed was 29.911 mm L_T in males and 31.909 mm L_T in females.

Of the 240 fish analysed, only 168 specimens (70%, 121 females and 47 males) could be sexually determined; the number of undetermined individuals decreased with increasing length. The overall sex ratio was significantly skewed to females (2.57 females/males, $p<0.05$). However, when the sex ratio was analysed per month, no significant differences were observed in January and February (Table 4).

Seasonal trends in gonad maturation, reproductive strategy and size at maturation

Spawning capable females (Fig. 5C) were observed from December to April, during the whole fishing season, with a peak in March (100%) (Fig. 4C, Table 5). When the fishing season ended, the fraction of females actively spawning was still 86.67%. Therefore, the beginning and the end of the spawning season were not detected in our sampling. Running males (M4, Fig. 5D) were found in December, January and February (Fig. 4D, Table 5). The number of sampled males in March and April was very low ($n=1$ and $n=5$, respectively), and ripe males were observed in both months. As in *Aphia minuta*, postspawning individuals were not observed. These observations indicated that the reproductive cycle of *Pseudaphia ferreri* was thus fairly synchronous at the population level, with most of the females actively spawning at the same time (in March) (Fig. 4C, Table 5).

Regarding ovarian development organization, *Pseudaphia ferreri* is a group-synchronous spawner: several batches of oocytes at different maturation stages could be observed at the same time in histological sections of spawning capable females (Fig. 5C), and the ovarian oocyte size-frequency distribution of *P. ferreri* (20-720 μ m oocyte diameter) showed a trimodal ovarian organization with three batches of oocytes (the last barely visible but present) separated by two hiatus ranging between 300-320 μ m and 680-700 μ m in size (Fig. 6B). Histological sections showed that *P. ferreri*

females also maintained a large reserve of PG oocytes in their ovaries (Fig. 5C) that would be recruited in a future spawning event, indicating iteroparity. Based on our results, *Pseudaphia ferreri* is an iteroparous batch spawner with determinate fecundity, since it maintains a standing stock of PG oocytes in its ovaries and develops different batches of vitellogenic oocytes to be released in the same spawning season. The smallest mature female was 18.219 mm L_T , and the size at 50% maturity was estimated at 21.405 mm L_T (logistic Model 95% CI=20.160-22.650 mm) (Fig. 7B). In the case of males, the smallest mature specimen was 21.673 mm L_T , and the size at 50% maturity was estimated at 21.871 mm L_T (logistic Model 95 CI=21.560–22.182 mm) (Fig. 7B).

Fecundity

Fp was estimated in 10 ovaries (corresponding to females ranging from 27.915 to 32.231 mm, L_T). It ranged between 1560 (in a female of 30.298 mm, L_T) and 4655 oocytes (in a female of 32.231 mm, L_T), with an average of 2516 oocytes (± 974 , sd).

Crystallogobius linearis

Length structure of the sampled population and sex ratio

Of the 132 specimens examined histologically, only 78 (59%) could be sexually determined by histological methods (41 females and 37 males). The overall sex ratio was slightly skewed to females, but no significant differences were observed ($p > 0.5$, Table 4). Only in April was the sex ratio significantly skewed to females (2.8 females/males). The L_T of the *C. linearis* sampled population ranged between 17.143 and 38.290 mm (Table 1, Fig. 2C), and the mean sizes increased from December to March in both sexes (Fig. 3), with males being significantly larger than females ($F = 35.630$, $p < 0.5$). Undetermined individuals were observed throughout the sampled population, decreasing slightly with increasing length (Fig. 2C). The maximum size observed was 38.290 mm L_T in males and 31.008 mm L_T in females.

Seasonal trends in gonad maturation, reproductive strategy and size at maturation

Spawning capable females, the most abundant developmental gonad stage (Fig. 4E) ranging between 82% and 93%, were observed in all the sampled months (Table 5), indicating population synchronicity. Immature females were not observed (Fig. 4E), whereas indeterminate individuals represented 41% of the sampling (Fig. 2C). As in *A. minuta* and *P. ferreri*, no postspawning individuals were observed. A peak of spawning activity was observed in April (92.86%). Running males (M4) were found from February to April and were more frequent in March (50%) (Fig. 4 F). It was not possible to determine the extension of

the spawning season because, although our sampling overlapped with it, it did not cover its whole range. Based on our histological observations, *Crystallogobius linearis* exhibited the reproductive strategy of an abbreviate iteroparous species because a reserve of PG oocytes is observed in spawning capable females (Fig. 5E, Fig. 6C). Similar to the females, spawning capable males exhibited active spermatogenic tubules (Fig. 5F).

The ovarian oocyte size-frequency distribution of *C. linearis* (20-640 μm oocyte diameter) showed a bimodal ovarian organization with two batches of oocytes separated by a large hiatus ranging between 260 and 340 μm in size (Fig. 6C), indicating determinate fecundity.

Furthermore, the species is an iteroparous total spawner: *C. linearis* females maintain a large reserve of PG oocytes in their ovaries, while the secondary growth oocytes have synchronous development in a single mode (Fig. 5E).

In relation to size at maturation, it was impossible to calculate L_{50} in females owing to the lack of immature females in the sampling. The smallest mature male was 20.964 mm L_T and 37 males (20.964-38.290 mm, L_T) were considered to estimate size at maturation. The size at 50% maturity in males was estimated as 21.716 mm L_T (logistic Model 95% CI=19.598-23.833; Fig. 7C).

Fecundity

Fp was estimated in 9 of the 10 selected ovaries (corresponding to females ranging from 24.364 to 30.561 mm L_T). The Fp ranged between 510 oocytes (in a female of 25.394 mm L_T) and 880 oocytes (in a female of 29.645 mm L_T), with an average of 644 oocytes (± 125 sd).

DISCUSSION

Length structure of the sampled population

During the sampled year, the average length per month (Fig. 3) of the sampled populations of *A. minuta*, *P. ferreri* and *C. linearis* confirmed that these populations are quite homogeneous in length according to their short lifespan of approximately one year (De Buen 1931). The largest sampled specimen of *A. minuta* was 40.682 mm L_T , which is considerably smaller than those described in the Adriatic Sea (57 mm, La Mesa et al. 2008) but similar to the maximum sizes described in the Majorcan fishery from 1985 to 1993 (Iglesias and Morales-Nin 2001). With respect to sex, males were significantly larger than females in *A. minuta* and *C. linearis*, as has been previously pointed out for other fisheries (La Mesa et al. 2001, 2005, Miller 1989) but not for this one (Iglesias and Morales-Nin 2001). Conversely, no significant differences were found in the mean L_T of males and females of *P. ferreri*; as far as we know, this is the first record of length-sex comparison in this species.

According to the literature, sex ratios from different populations of *A. minuta* showed marked interannual variability both calculated on an annual and a monthly

basis, although both sexes are present year round (Martínez-Baño et al. 1993, Iglesias and Morales-Nin, 2001, La Mesa et al. 2005). *A. minuta* females are more abundant in winter and early spring, with the sex ratio close to 1:1 in the other months (La Mesa et al. 2005). Our data support these previous findings, as females of *A. minuta* were more abundant during the whole sampled fishing season. Similar results were observed in *P. ferreri* and *C. linearis*, although significant differences were not detected in the latter species. These differences in the sex ratio could be explained by differential maturity rates that condition the aggregation of individuals ready to reproduce (Iglesias and Morales-Nin 2001). Accordingly, in *Aphia minuta*, females grow faster than males, although males eventually become larger (Iglesias et al. 1997).

Interestingly, despite using histological methods, in part of the sampled population of the three studied species the sex could not be determined, although the proportion decreased with increasing size. Nevertheless, our gonad microscopic study provided a more accurate result than traditional macroscopic approximations, explaining the lower proportion of indeterminate individuals in our study than in previous ones (Iglesias and Morales-Nin 2001). As the gonads are not microscopically detected in two cross-sections of the whole individual, it is very likely that these indeterminate individuals corresponded to immature specimens (in phase 1 in both sexes). Therefore, a non-negligible part of the exploited schools (in the three species) could have been formed by immature individuals, especially at the beginning of the fishing season (Iglesias and Morales-Nin 2001), which would agree with the migratory schooling behaviour previously proposed (La Mesa et al. 2005).

Reproductive strategy and reproductive cycle

Our histological study confirmed abbreviate iteroparity as a reproductive strategy in all three species. Iteroparous species maintain a reserve of PG oocytes and have the potential to participate in different reproductive cycles (Lowerre-Barbieri et al. 2011a). Accordingly, histological examination of the ovaries of the three studied species revealed the presence of a considerable reserve of PG oocytes, which implies that they can potentially participate in more than one reproductive cycle. In contrast, semelparous species have no need for such a reserve and exhibit total recruitment of all PG oocytes to secondary growth (Lowerre-Barbieri et al. 2011b).

With respect to *Aphia minuta*, abbreviate iteroparity has been previously pointed out (Caputo et al. 2000). Interestingly, through back-calculation hatch dates Iglesias and Morales-Nin (2001) detected continuum spawning events throughout the year with two spawning peaks (in March and October). These observations led them to hypothesize the existence of two annual cohorts assuming semelparity in *Aphia minuta*, which implies participation of each individual in only one reproductive cycle followed by death. However, abbreviate iteroparity implies that the same individual

could participate in more than one spawning season in its short lifespan. Additionally, our histological study revealed *A. minuta* as a batch spawner because mature ovaries contained batches (at least three) of secondary growth oocytes in different development stages to be spawned in the current spawning season. This also implied that the same individual could participate in multiple spawning events per spawning season. Moreover, our study revealed that *Aphia minuta* displays spawning asynchrony at the population level, a common fact in warm water habitats (Lowerre-barbieri et al. 2011b). Altogether, these features explained the continuous spawning season detected by back-calculation (Iglesias and Morales-Nin 2001) and evidenced a more complex scenario than was initially supposed (involving more than one spawning event and more than one spawning season per individual together with population asynchrony). Considering that our A_{50} estimations for the species were 105 days for females (3.5 months) and 199 days for males (6-7 months), the hypothesis of three spawning peaks—one in March observed by us, one in June-July deducted from the A_{50} of females and one in September-October obtained by back-calculation by Iglesias et al. (2001)—could be considered plausible. This hypothesis would match the spawning season observed by Caputo et al. (2000) in the central Adriatic Sea.

Our results also showed *Pseudaphia ferreri* to be an abbreviate iteroparous species and a batch spawner with a reproductive strategy similar to that of *A. minuta* (discontinuous oocyte recruitment and determinate fecundity). Interestingly, *Crystallogobius linearis* is also an abbreviate iteroparous species because it maintains a reserve of PG oocytes in its gonads, but its spawning pattern matches that of a total spawner because secondary growth oocytes have relatively synchronous development in a single cohort (Fig. 5E), which will be spawned in only one event or over a short period of time. Conversely, Caputo et al. (2003) pointed out semelparity as a reproductive strategy for *C. linearis*, arguing that the proportion of PG oocytes was very low. Semelparous species, which participate in only one reproductive event and then die, never maintained a reserve of PG oocytes, recruiting all their oocytes into secondary growth (Lowerre-Barbieri et al. 2011a). Furthermore, the current study reveals a much larger proportion of PG oocytes than that reported by Caputo et al. (2003).

The impossibility of obtaining samples throughout the year due to legal restrictions (Decree 46/2013 and Decree 31/2021) prevented us from completing the annual reproductive cycle of the three species and even their whole reproductive season. However, spawning peaks were observed in March for *A. minuta* and *P. ferreri* and in April for *C. linearis* (although the percentage of spawning females for this species remained almost constant throughout the sampling). The spawning peak and spawning season in *Aphia minuta* coincide with previous data from the fishery (from January to April; Iglesias and Morales-Nin 2001). There are no data available on the spawning season of the other two species in the Majorcan transparent goby fishery, or in

any other in the case of *P. ferreri*, ours being the first data available. With respect to *C. linearis*, La Mesa (2001) indicated a long breeding season for the species (from October to May with a main peak in January) by back-calculation techniques in the central Adriatic Sea. Our results revealed differences between those of La Mesa (spawning season at least from January to April with an extended spawning peak). Interestingly, our results reveal that the spawning season of *Pseudaphia ferreri* extends throughout the fishing season, from December to April, peaking in March (100% spawning capable females at this month). Therefore, in all three species, the spawning season has not ended when the legal closure of the fishery occurs, which means that long breeding seasons extended beyond the last sampling month. Extended seasons are more common in warm water habitats (Pavlov et al. 2009) and provide a greater number of reproductive opportunities, which have the potential to increase recruitment (James et al. 2003). This fact may help counteract the sensitivity to environmental changes shown by these progenetic populations formed by individuals of only the one-year class.

Maturity

Based on histological methods, our study determined the length at maturity of the three progenetic gobies targeted by the small-scale Majorcan fishery. The size at first maturity of *Pseudaphia ferreri* was similar in males and females (21.871 mm and 21.405 mm, respectively), confirming the homogeneity in maturity of the population. However, in *A. minuta* the size at maturity was quite different for females and males: 28.457 mm and 35.116, respectively. These results were considerably lower than those reported by Iglesias and Morales-Nin (2001) for the same fishery (males 34 mm L_T ; females 38 mm L_T), probably as a consequence of the use of macroscopic staging, but are in agreement with the differential growth and maturity rates between sexes noted by Iglesias et al. (1997) and Iglesias and Morales-Nin (2001).

Regarding *C. linearis*, only size at maturity for females has been reported in the central Adriatic Sea by macroscopic observation (27.4 mm; Caputo et al. 2003). However, in our study, size at maturity was histologically determined only in males (21.716 mm L_T). Estimates of size at 50% maturity depend on the methodology used (macroscopic vs. histological techniques), the number and size range of the sample, and the sampling period considered in the estimations (Hunter et al. 1992), in addition to the environmental conditions and fishing effort, making it difficult to draw conclusions.

Fecundity

Fp in *Aphia minuta* ranged between 1746 and 6600 oocytes (mean 3609.87 ± 1134.42 sd; 0.020-0.880 mm oocyte diameter). This result was similar to that estimated in the Adriatic Sea (1500-7000 oocytes; Froggla and Grammito 1989) and in the

central Tyrrhenian Sea (2500-5000 oocytes; Auteri et al. 2000). However, our results were considerably higher than those previously reported for the same fishery (900-2700 oocytes with an oocyte diameter of 0.120-0.600 mm; Iglesias and Morales-Nin 2001). Considering the differences in size between the two measurements, it is very likely that Iglesias and Morales-Nin (2001) underestimated Fp by discarding smaller oocytes. Furthermore, Iglesias and Morales-Nin (2001) estimated fecundity in females captured in March. According to our results, the species is at its maximum spawning peak in that month. Taking into account that in determinate spawners fecundity must be estimated from prespawning ovaries (Murua et al. 2003), an underestimation of the previously calculated Fp is plausible.

To the best of our knowledge, the Fp of *P. ferreri* and *C. linearis* were estimated for the first time. The Fp of *P. ferreri* ranged between 1560 and 4655 oocytes, similar to the Fp of *A. minuta*. Conversely, the Fp of *C. linearis* was lower than that of the other gobies of the fishery, ranging between 510 and 880 oocytes, which suggests a lower recruitment capacity than the other ones.

Management implications and conclusions

For all three species, our data revealed that the winter-spring spawning season is longer than the fishing season and that individuals of all three species have more than one spawning season in their short lifespans. These characteristics favour the sustainability of the fishery since, although the winter-spring reproductive aggregations are fished in the three species, their spawning seasons temporarily exceed the fishing season, to which is added the existence of another spawning season in its short life, completely outside the fishing season. Consequently, within the regulatory framework of the Management Plan for Fishing with Traditional Boat Seines in the waters of the Balearic Islands (Decree 46/2013 and Decree 31/2021), it makes sense for all three species to maintain the seasonal closure of the *A. minuta* fishery, as currently regulated, to protect their spawning events from May to December.

While there is reasonable knowledge about the life cycle and reproductive characteristics of *A. minuta* (although very little is known about its migration and distribution), there are many gaps in the knowledge of the other two species of the fishery: *P. ferreri* and *C. linearis*. Currently, the main problem in the Majorcan transparent goby fishery has been the decreasing abundance of *A. minuta* in the landings and its replacement with *P. ferreri*, a less appreciated species. If only *A. minuta* fishing had been taken into account in the fishing monitoring, the administration would have had to adopt restrictive measures (Morales-Nin et al. 2022). The causes of this change are unknown, and only speculative hypotheses such as environmental changes can be put forward. It is therefore mandatory to continue improving knowledge on the biology of these species in order to optimize the management of

the transparent goby fishery without compromising its sustainability.

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