Reproductive biology of pollack (*Pollachius pollachius)* from the Galician shelf (north-west Spain)

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The pollack, Pollachius pollachius*, is an important commercial species for the Spanish artisanal fleet in Atlantic Iberian waters. This study provides information on the reproductive biology of the species, including length at maturity, reproductive cycle and gamete development pattern based on histological methods. A collection of 622 individuals were sampled from fish markets along the western coast of Galicia (NW Spain), between November 2009 and October 2010. Histological examination of the gonads revealed an asynchronous development of secondary growth follicles. Testicular tissue was of lobular type. The reproductive season extended from January to April for females and from January to May for males, with a peak of reproductive activity in February for both sexes. The hepatosomatic index was related to the reproductive cycle, with a mean maximum value during the developing reproductive phase. Length at 50% maturity was significantly different between females (47.1 cm) and males (36.1 cm).*

INTRODUCTION

Pollack, *Pollachius pollachius* (Linnaeus, 1758) (Gadidae) is distributed widely in the NE Atlantic from northern Norway to North Africa (Cohen *et al.*, 1990). *Pollachius pollachius* is the largest of the eight gadoid species occurring in Galician waters (Bañon *et al.*, 2010). This species is targeted mainly by the artisanal fleet, basically with gillnets and lines, in coastal areas, although it is occasionally caught as by-catch in offshore trawl fisheries (Rodriguez *et al.*, 2011). Unlike other exploited gadoids, such as cod, *Gadus morhua* and saithe, *Pollachius virens*, the biology of *P. pollachius* remains poorly known. Previous reproductive studies were limited in scope and/or focused mainly on controlled experiments for aquaculture purposes (Suquet *et al.*, 1996, 2005; Omnes *et al.*, 2002). In spite of its importance as a fishery resource throughout much of its distribution range (ICES, 2010), there is no assessment for *P. pollachius* in ICES Division VIIIc (where Galician waters are included). In these areas, management conservation is based on total allowable catch (TAC) which are based on landings trends. Recently, *P. pollachius* was included in a list of stock and species for which collecting data might be required to better evaluate stock status (ICES, 2010; Rodriguez *et al.*, 2011). As a starting point, biological data are being collected for the species following a European commission decision (European

Union, 2010). However, the information available to date is still insufficient to evaluate the *P. pollachius* stock status in Galician waters.

The capacity of a population to produce viable eggs and larvae is important in the recruitment process of exploited fish stocks (Solemdal, 1997; Marteinsdottir & Steinarsson, 1998; Kraus *et al.*, 2002). The understanding of these processes has acquired increasing notoriety over the past decade, after the validity of traditional indicators like spawning stock biomass began to be questioned (Marshall *et al.*, 1998). All these considerations that affect population dynamics are encompassed by the term stock reproductive potential, introduced by Trippel (1999). Reproductive biology has a crucial role in fishery stock assessment of the productivity of exploited stocks. Its integration into advice and management strategies is expanding through the production of alternative indices of reproductive potential (Trippel, 1999; Morgan, 2008). Thus, improved estimates of population reproductive potential should lead to enhanced performance of the models used in some fisheries assessments (Marshall *et al.*, 1998). For example, several reproductive traits like sex-ratio, maturity or fecundity have been suggested to be included in sampling programmes for fisheries assessment (Tomkiewicz *et al.*, 2003; Lambert, 2008; Morgan, 2008). An accurate evaluation of the gonad development is crucial to describe the maturation process, the timing of reproduction or follicle recruitment process (Murua & Saborido-Rey, 2003; Lowerre-Barbieri *et al.*, 2011b). Age/ size at maturity is the most common and well-studied life history parameter in fish exploited populations, mainly

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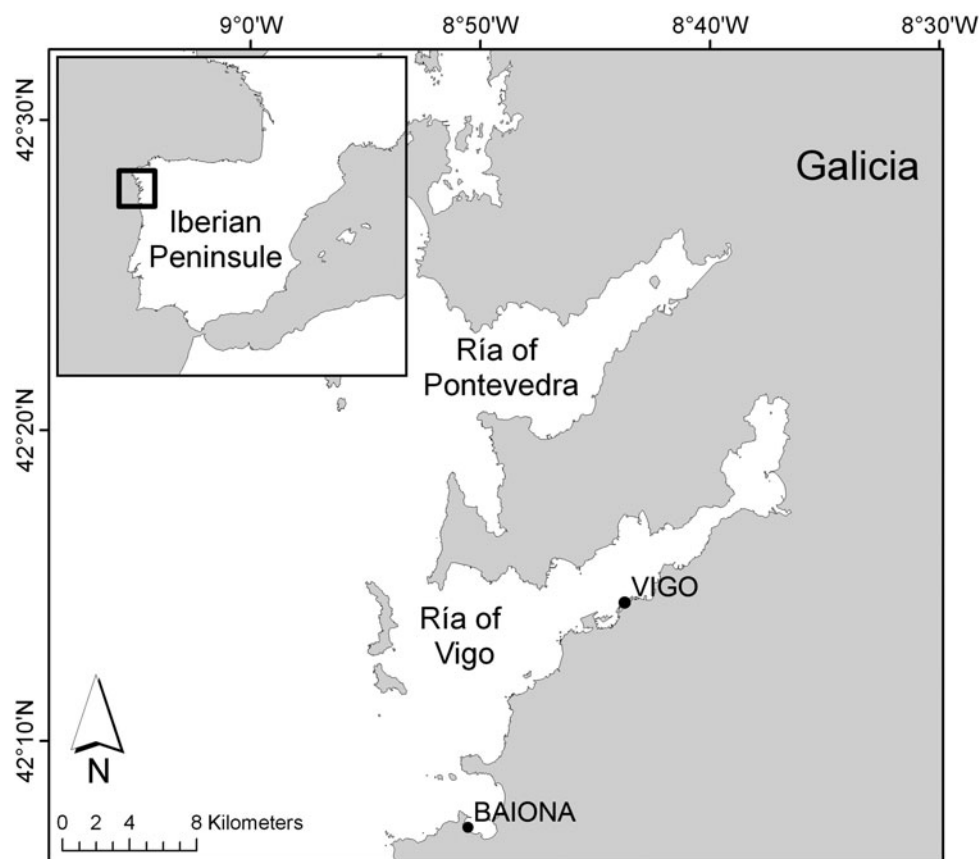A. Alonso-Fernández
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Fig. 1. Study area, the western coast of Galicia, showing locations of fish markets used to sample *Pollachius pollachius*.

used in stock assessment to get a better estimation of limit reference points (Morgan, 2008). Additionally, atresia levels have been used as a criterion for determination of fecundity strategies, i.e. determinate vs indeterminate (Greer Walker *et al.*, 1994; Alonso-Fernández *et al.*, 2008; Ganias, 2013). The timing and length of the spawning season have long been recognized as critical factors in the recruitment process, since they determine the likelihood of eggs and larvae to find suitable environmental conditions for their survival (Cushing, 1972; Mertz & Myers, 1994; Alonso-Fernández & Saborido-Rey, 2011). Traditionally, studies of reproductive biology have assumed that most of the variations in population reproductive success are attributable to maternal effects (Solemdal, 1997). Thus, most of the literature on reproductive potential of fish populations has focused mainly on females (Murua & Saborido-Rey, 2003). In the last decades, however, there has been an emerging interest in male effects of reproductive potential (Trippel, 2003), the *paternal effect*, for which a basic knowledge of male reproductive biology is required.

This study aimed to improve our knowledge of the reproductive biology of *P. pollachius* in an area in the southern part of its geographical range. Several important reproductive traits are described for the first time in a wild population of *P. pollachius*. Specifically, the objectives of this study were: (1) to describe the gamete development pattern and gonad organization; (2) to characterize the reproductive cycle and prevalence of atresia; and (3) to estimate the length at maturity for males and females in

Galician waters. These results will help provide information for any future stock assessment.

MATERIALS AND METHODS

A total of 622 individuals were obtained on a monthly basis from the fish markets along the western coast of Galicia (Atlantic Iberian waters, ICES Division VIIIc, Figure 1) between November 2009 and October 2010, with the exception of August 2010 (Table 1). Fish were kept refrigerated until processing, with tissues sampled within 12 hours.

Table 1. Monthly distribution of the sample size (number of individuals) and mean ($\pm$ SD) fish total length (cm) and eviscerated weight (g) of *Pollachius pollachius* from the western coast of Galicia.

Year	Month	Sample size	Total length	Eviscerated weight
2009	November	56	52.8 $\pm$ 9.8	1562.0 $\pm$ 792.5
	December	7	39.9 $\pm$ 9.0	636.2 $\pm$ 356.5
2010	January	36	56.0 $\pm$ 10.2	1765.9 $\pm$ 1168.6
	February	47	52.0 $\pm$ 14.5	1587.1 $\pm$ 1141.2
	March	211	50.2 $\pm$ 14.8	1400.4 $\pm$ 972.4
	April	82	45.0 $\pm$ 16.4	1142.5 $\pm$ 1249.0
	May	36	56.8 $\pm$ 11.9	1929.3 $\pm$ 1356.7
	June	46	61.7 $\pm$ 7.7	2223.1 $\pm$ 901.5
	July	23	64.9 $\pm$ 5.0	2617.1 $\pm$ 569.6
	August	–	–	–
	September	22	60.6 $\pm$ 7.1	2172.2 $\pm$ 688.7
	October	56	58.5 $\pm$ 13.0	2142.4 $\pm$ 1201.5
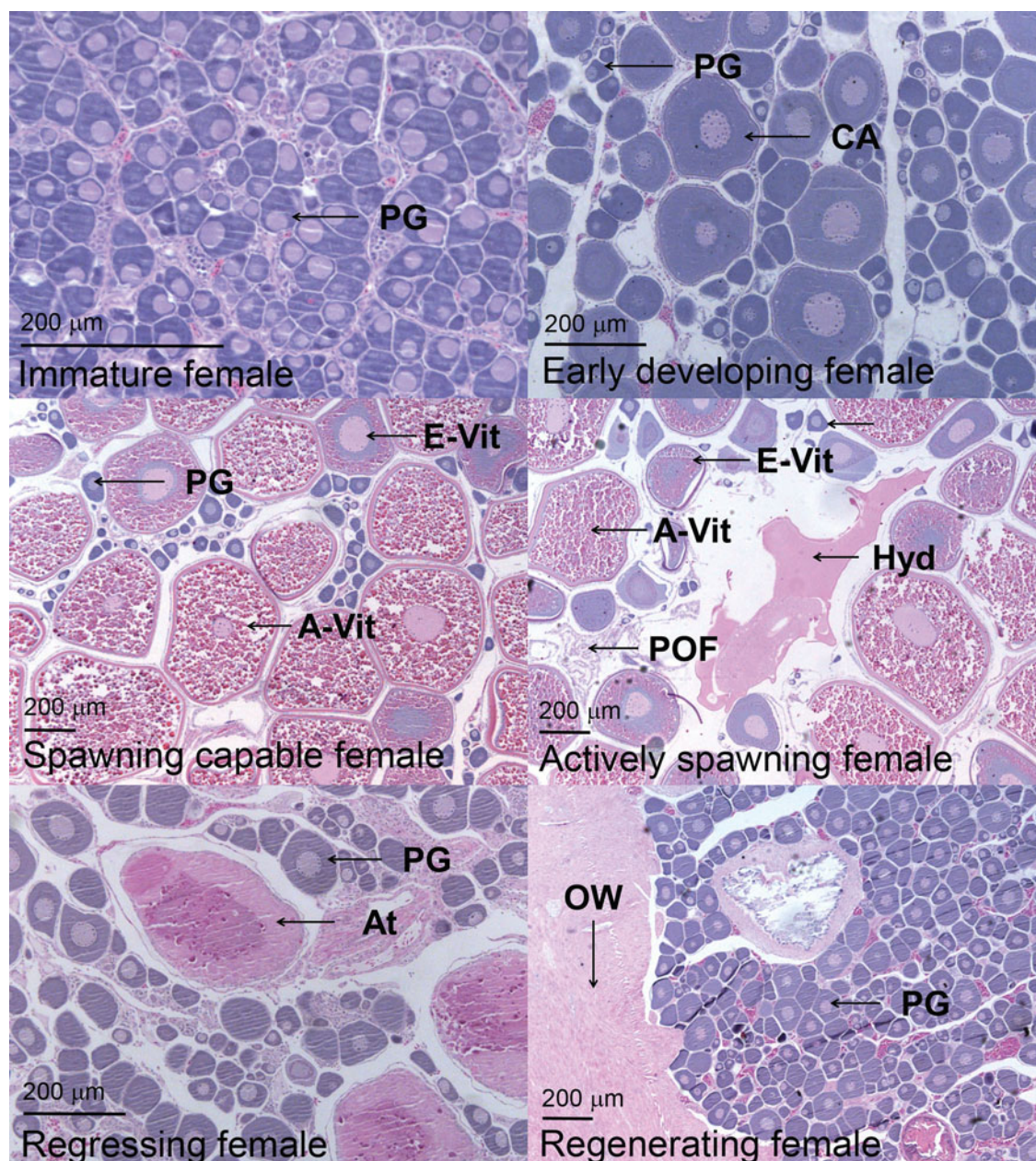
Fig. 2. Female reproductive phases of *Pollachius pollachius*. Follicle development stages and other gonad structures presented in the ovaries: PG, primary growth; CA, cortical alveoli; E-Vit, early vitelogenesis; A-Vit, advanced vitelogenesis; Hyd, hydrated follicle; POF, post ovulatory follicles; At, atretic follicles; Cys, cystic follicles; OW, ovary wall.

Data collection

The following parameters were recorded for each fish: total length (L_T, $\pm$ 0.1 cm), total weight (W_T, $\pm$ 0.01 g), eviscerated weight (W_E, $\pm$ 0.01 g); sex; reproductive phase; gonad weight (W_G, $\pm$ 0.01 g) and liver weight (W_L, $\pm$ 0.01 g).

Gonads and livers were removed and three indices were estimated for each mature fish: gonadosomatic index (GSI), hepatosomatic index (HSI) and Fulton's condition factor (K).

$$\mathrm{GSI} = 100^* W_G / W_E$$
$$\mathrm{HSI} = 100^* W_L / W_E$$
$$\mathrm{K} = 100^* W_E / L_T^3$$

Gonads from all specimens were fixed in 10% formalin, buffered with $Na_2HPO_4{}^*2H_2O$ (0.046 M, molar concentration) and $NaH_2PO_4{}^*H_2O$ (0.029 M) for histological processing. Central portions of the fixed gonads were extracted, dehydrated, embedded in paraffin, sectioned at 3 μm and stained with haematoxylin–eosin for microscopic analysis.

For each ovary, the follicles were classified into stages of development according to histological criteria: primary growth, cortical alveoli, vitellogenesis, germinal vesicle migration and hydration (West, 1990; Tyler & Sumpter, 1996; Brown-Peterson *et al.*, 2011). Atretic follicles were detected in ovarian histological samples (presence–absence) in order to assess the portion of fish with atresia. Thus, only
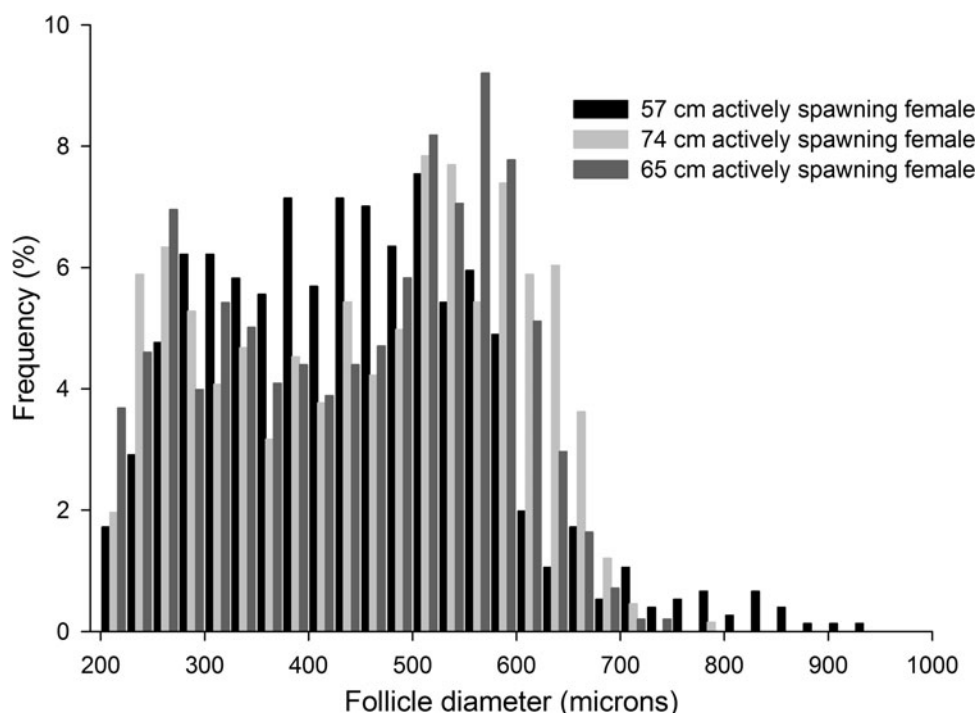
Fig. 3. Size–frequency distribution of follicles for three actively spawning females of *Pollachius pollachius* (total length of females is shown in the legend). Only developing follicles (>200 μm) are represented.

one of the three indices of atresia proposed by Kurita *et al.* (2003) was estimated; the prevalence of atresia, as the number of mature female pollack showing follicular atresia divided by the total number of mature females. In male pollack, testicular tissue germ cells were classified into the following stages of development: spermatogonia, spermatocysts, spermatids and spermatozoa (Grier, 1981). This allowed each fish, males and females, to be classified in one of the following reproductive phases: immature, developing, spawning capable and correspondent sub-phases actively spawning, regressing and regenerating (Brown-Peterson *et al.*, 2011).

Cortical alveoli follicles ($N = 110$) were measured in histological sections of nine females to establish their threshold size, in order to identify the size above which is the stock of developing follicles in the ovaries (μm, mean ± SD = 218 ± 29). To study follicle size–frequency distribution and ovarian development organization of secondary growth follicles, the number and size of developing follicles (follicle development gonadotropin dependent phases: from cortical alveoli to final maturation) (Wallace & Selman, 1981; Lubzens *et al.*, 2010) were assessed in three actively spawning females. After being separated from the connective tissue (Lowerre-Barbieri & Barbieri, 1993), follicles were counted and measured in whole mount samples (~50 mg from the central portion of the ovary) with image analysis software (Leica QWin) on a PC connected to a video camera (Leica DFC490) connected to a stereo microscope (Leica Z6 APOA).

Data analysis

All statistical analyses were conducted in R software (R Development Core Team, 2011). Only data from specimens where sex was confirmed histologically were used in the data analysis (304 females, 194 males).

The female reproductive cycle of *P. pollachius* was evaluated based on the monthly variation of the mean GSI values and frequencies of reproductive phases. Besides the GSI, other somatic indices can be useful to evaluate seasonal fluctuations in energy reserves related to gonadal development and reproductive activity (Henderson *et al.*, 1996; Lambert & Dutil, 2000; Alonso-Fernández & Saborido-Rey, 2012). The HSI and K were used as proxies of available energy reserves in liver and somatic tissue, respectively. To reduce the effect of the presence of different reproductive phases in each month and to properly depict the relationship of these indices with the reproductive cycle, the variation in the mean values of somatic indices between reproductive phases was assessed. Differences in GSI, HSI and K during the year and between reproductive phases were statistically evaluated using generalized least squares (GLS) models (Pinheiro *et al.*, 2010) to account for heterogeneity problems (Zuur *et al.*, 2009).

Length at maturity ($L_{50\%}$), defined as the body length at which 50% of the individuals were mature, was obtained by using generalized linear models (GLM) (McCullagh & Nelder, 1989) with a binomial family distribution. Sex of the individuals was included as a factor in the model to account for differences in maturation between males and females. $L_{50\%}$ estimations and their uncertainties were estimated employing the non-parametric bootstrap method (Efron, 1979). In addition, a graphical comparison of maturity ogives parameters was made using the techniques of Kimura (1980) for comparison of growth parameters. This technique consisted of generating 95% confidence ellipses around the parameter estimated by the GLM (Murdoch & Chow, 2007). Non-overlapping confidence regions indicated differences in maturity ogive parameters.
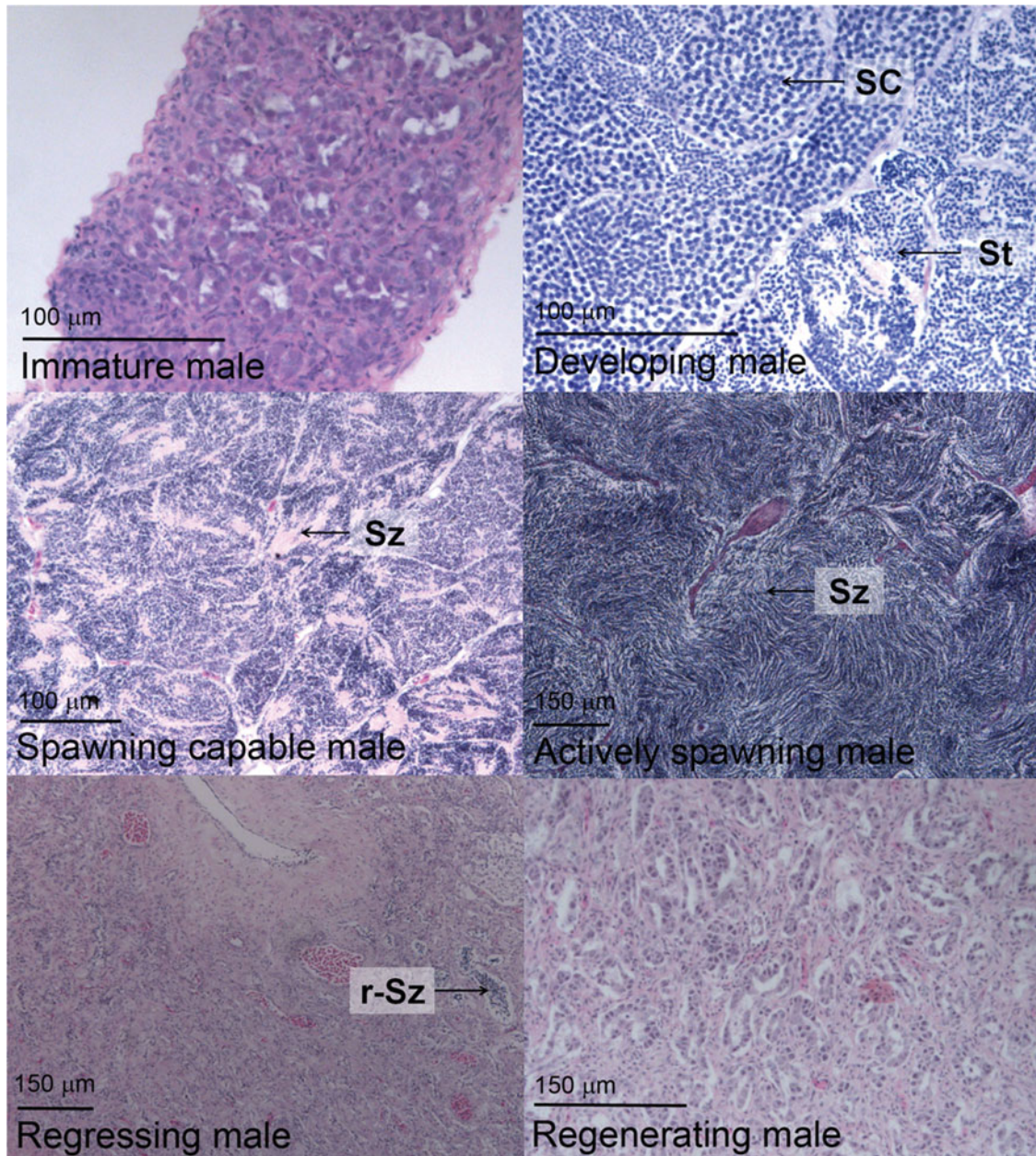
Fig. 4. Male reproductive phases of *Pollachius pollachius*. Spermatogenesis development stages present in the testis: Sc, spermatocyst; St, spermatid; Sz, spermatozoa; r-Sz, residual spermatozoa.

RESULTS

Ovarian and testicular development organization

The ovaries of *Pollachius pollachius* are oval-shaped, with the two lobular ovaries partially fused, each one with a roughly hollow cylindrical form and a lamellar internal configuration. Folliculogenesis followed the process of follicle maturation common to other teleosts: primary growth, cortical alveoli, vitellogenesis, migratory nucleus (Wallace & Selman, 1981; Guraya, 1986; Tyler & Sumpter, 1996). Follicle maturation ends with hydration of follicles, leading then to ovulation (Lowerre-Barbieri *et al.*, 2011b). The nucleus was not displaced by an oil droplet formation.

Pollachius pollachius exhibited an asynchronous development of secondary growth follicles, i.e. secondary growth follicles of all stages of development were present without a dominant population (Figure 2). This asynchrony was reflected by the follicle size–frequency distribution in the spawning capable phase, with no gap among primary growth and developing follicles (Figure 3). There was a continuous follicle size–frequency distribution, with the exception of such ovaries with hydrated follicles, which had a separate mode of large hydrated follicles. Several modes were present within the continuous follicle size–frequency distribution.

The histological structure of the testis of *P. pollachius* showed a lobular type. Spermatogonia were distributed randomly along the entire length of the tubule in reproductive active fish. Spermatogenesis occurred within germinal cysts
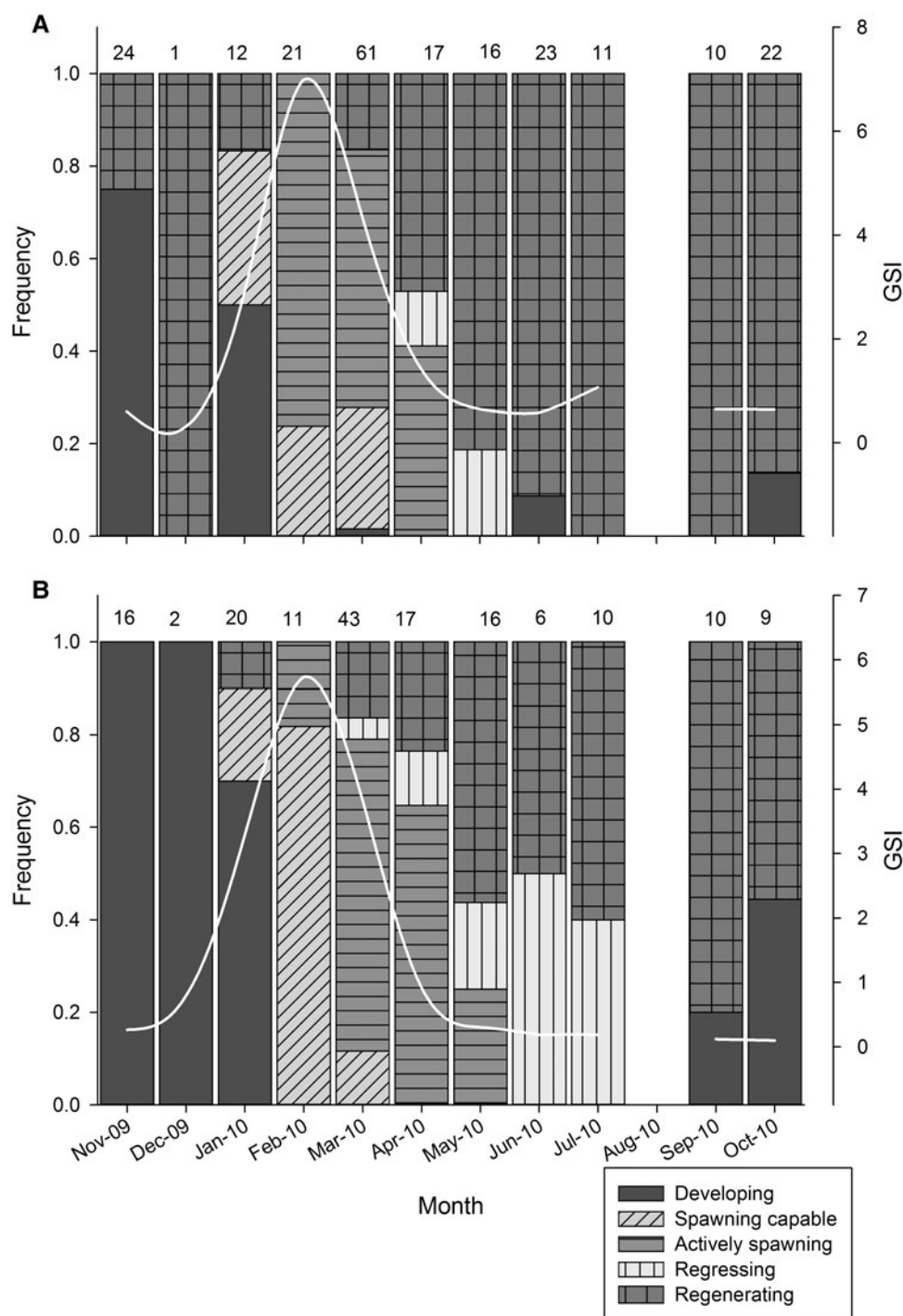
Fig. 5. Frequency of reproductive phases for (A) female and (B) male *Pollachius pollachius*. White line represents variation of mean GSI (gonadosomatic index) value through the year. Numbers on bars represent the number of individuals. *X* axis labels indicate month and year of sampling.

formed by enveloping Sertoli cell cytoplasmic processes; within each cyst, the maturation of germ cells was synchronous (Grier, 1980, 1981) (Figure 4).

Reproductive cycle

Values of GSI for both sexes peaked in February. Accordingly, 100% of mature females were classified as spawning capable (including actively spawning) in that month (Figure 5). Reproductive phase frequencies also revealed some reproductive activity in the gonads of females from January to April (spawning capable frequencies, including actively spawning: 26.67% in January, 76.93% in March and 26.92% in April). The largest proportion of regressing females was found in April and May (7.69% and 15.0%, respectively). The prevalence of atresia was highest in April (34.62%) and May (25%), and in regressing individuals (Figure 6). Male reproductive cycle extended from January to May, with a peak of reproductive activity in February. The largest proportion of regressing males was found in June (50%).
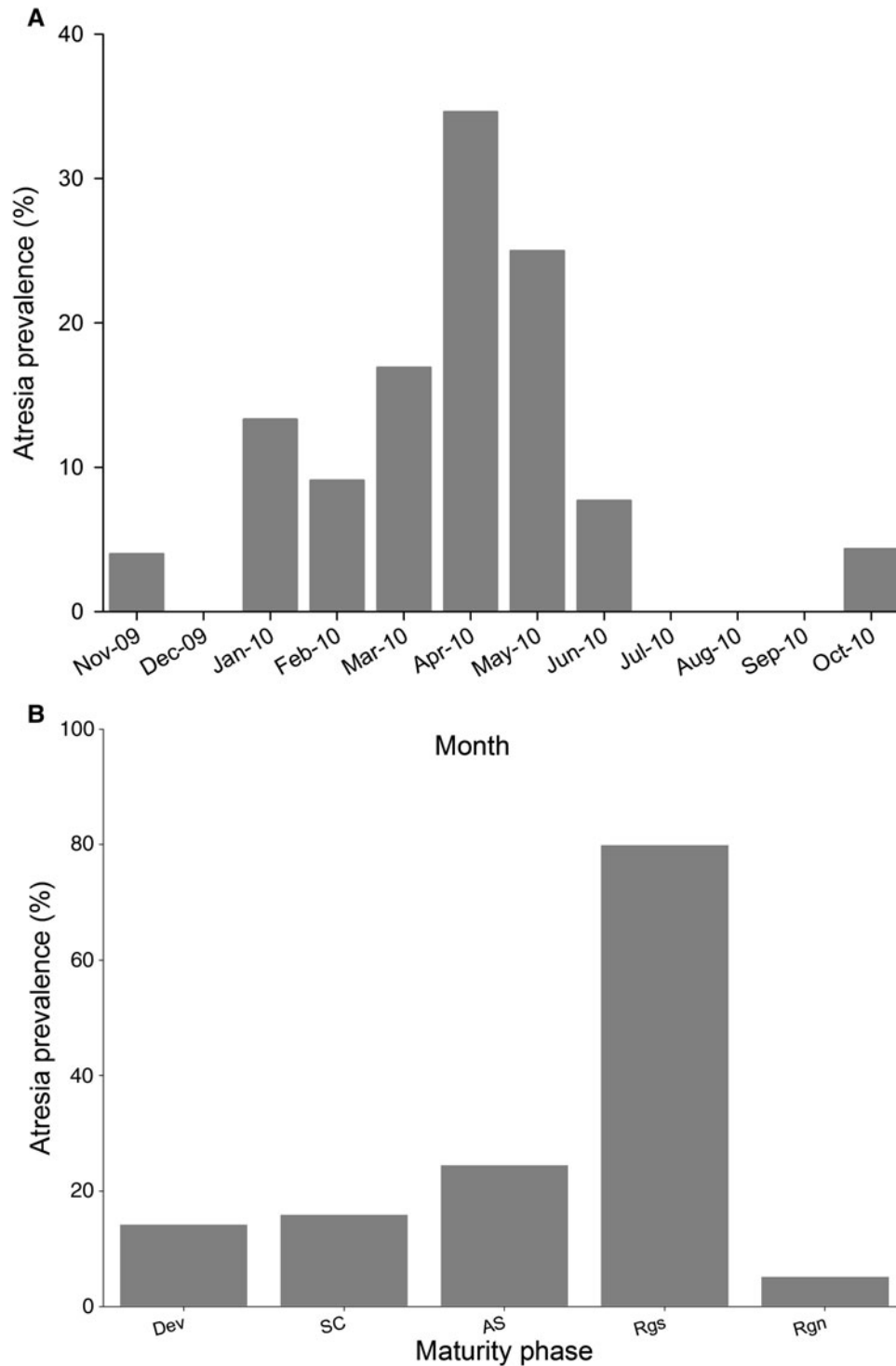
Fig. 6. Prevalence of atresia in ovaries (A) along the year and (B) in different reproductive phases of *Pollachius pollachius*. Maturity phases are denoted as follows: Dev, developing; SC, spawning capable; AS, sub-phase actively spawning; Rgs, regressing and Rgn, regenerating. *X* axis labels indicate month and year of sampling.

Average values of GSI, HSI and K varied significantly during seasonal reproduction and sexes (Table 2). All the three indices dropped to minimum values in March/April in females, extending to May in the case of males (Figure 7). Maximum HSI levels occurred in October for females and November for males. K was at a maximum in November for both sexes.

Variation of GSI, HSI and K among the different reproductive phases and sexes was also significant (Table 3). Maximum values of GSI were observed in actively spawning females and males (Figure 7), and minimum values in the regenerating phase. For the HSI, minimum values corresponded with the actively spawning sub-phase in both sexes and maximum values occurred in the developing phase (Figure 7). In the case of K, maximum value was found in the regressing phase for females and in the developing phase for males. The minimum was located in the spawning capable phase for males and in the actively spawning sub-phase in females (Figure 7).

Table 2. Seasonal variation of somatic indices of *Pollachius pollachius* from the western coast of Galicia. Summary of multiple general least squares (GLS). GSI, gonadosomatic index; HIS, hepatosomatic index; K, condition factor. Note that the symbol ':' denotes interaction and df means degrees of freedom.

Index		df	F value	P value
GSI	Intercept	1	1602.39	<.0001
$N = 376$	month	10	66.35	<.0001
$r^2 = 0.59$	sex	1	415.49	<.0001
	month:sex	10	1.98	0.034
HSI	Intercept	1	4759.03	<.0001
$N = 378$	month	10	20.28	<.0001
$r^2 = 0.40$	sex	1	39.15	<.0001
	month:sex	10	2.22	0.0163
K	Intercept	1	97,479.43	<.0001
$N = 378$	month	10	8.36	<.0001
$r^2 = 0.13$	sex	1	5.81	0.0164
	month:sex	–	–	–

Length at sexual maturity

Maturity ogives for males and females displayed a similar shape (Figure 8). Nonetheless, estimates of $L_{50\%}$ revealed significant differences between males and females, being 36.1 cm and 47.1 cm, respectively. The smallest mature fish found were a 26.8 cm male and a 42 cm female and the largest immature fish were a 47.3 cm male and a 66 cm female. Variation in maturity ogives was due mainly to the intercept of the relationship (Table 4; Figure 8). $L_{50\%}$ for the sexes combined was 42.3 cm.

DISCUSSION

Pollachius pollachius is a widely distributed species on European coasts and although there are reports of *P. pollachius* landings in Spanish waters (Rodriguez et al., 2011), little biological information is available for this species in the southern parts of its geographical range. Therefore, the present study presents the first data for reproductive biology of this species in Galician waters, which will be informative for any future stock assessment and fishery management (Marshall et al., 2003; Morgan, 2008; Lowerre-Barbieri et al., 2011b), but also for aquaculture purposes (Suquet et al., 1996; Omnes et al., 2002).

Proper knowledge of gametogenesis represents a main goal in comprehending fish reproductive strategies (Murua & Saborido-Rey, 2003). Thus, an accurate evaluation of ovarian development is crucial to describe the maturation process, the timing of reproduction or the follicle recruitment (Lowerre-Barbieri et al., 2011a). Histological examination of the gonads revealed that *P. pollachius* presented asynchronous development of secondary growth follicles, i.e. follicles of all stages of development were present without dominant cohorts. This was confirmed by the continuous follicle-size distribution which is a distinct evidence of asynchronous development of secondary growth follicles (Wallace & Selman, 1981; Murua & Saborido-Rey, 2003). Asynchronous development of secondary growth follicles is usually associated with species of indeterminate fecundity (Murua & Saborido-Rey, 2003). However, determinate fecundity

strategies have been proposed in certain asynchronous species including Atlantic mackerel, *Scomber scombrus* (Greer Walker et al., 1994), brown meager, *Sciaena umbra* (Grau et al., 2009) and bib, *Trisopterus luscus* (Alonso-Fernández et al., 2008). However, further research on follicle recruitment process is required to accurately determine the fecundity type of *P. pollachius*. Although this study did not address egg production, histological examination of the ovaries indicated that *P. pollachius* is a batch spawner. Presence of post-ovulatory follicles in the spawning capable females and the presence of several modes in the developing follicle pool are clear evidences of batch spawning type (Murua & Motos, 2006). This fact is in agreement with previous studies of *P. pollachius* spawning type in captivity (Suquet et al., 1996; Omnes et al., 2002).

In males the three major phases composing spermatogenesis were present in *P. pollachius*: mitotic proliferation of spermatogonia, meiosis of spermatocytes, and spermiogenesis, the restructuring of spermatids into flagellated spermatozoa (Schulz & Miura, 2002). Testicular tissue is of the lobular type (Takashima & Hibiya, 1995), i.e. spermatogonia are randomly distributed along the entire length of the lobule in reproductive active fish, which is equivalent to the unrestricted spermatogonial type (Grier, 1980, 1981). Spermatogenesis is cystic in this species, thus, developing germ cells are enclosed within germinal cysts formed by enveloping Sertoli cells.

This study represented the first approach in Atlantic Iberian waters to the annual reproductive cycle of *P. pollachius*. Some females with reproductive activity were detected from January to May, with a peak of spawning in February (more than 70% of mature females in active spawning condition), as confirmed by both histology and GSI mean values variation. In captive fish from wild populations, previous estimations of female spawning season are relatively far from our results, with estimated durations of 92 days at $9.5–11.8°C$ (Suquet et al., 1996), 57 days at $9.0–11.5°C$ (Omnes et al., 2002) and 65 days at $8.0°C$ (Suquet et al., 2005). Our estimation of the spawning season duration (around 4 months) was shorter than that of other gadoids in Spanish waters, such as *T. luscus* (Alonso-Fernández et al., 2008), but closer to other gadoids such as Norway pout *Trisopterus esmarkii*, poor cod *Trisopterus minutus* and whiting *Merlangius merlangus*, with reported spawning seasons of around 3–4 months (Cooper, 1983).

In spite of the observed differences in the mean GSI values of males and females, male reproductive cycle followed the same seasonality as females but extended until the end of May. Longer duration of male reproductive season may guarantee in some way the reproductive success of the species. This is the case of other exploited fish species like cod, *G. morhua* (Hutchings & Myers, 1993), anglerfish, *Lophiomus setigerus* (Yoneda et al., 1998) and winter flounder, *Pleuronectes americanus* (Sonya & Burton, 1999). An extended duration of spawning capable activity in males compared to those of females is usually a characteristic of batch spawning fish, in which spermatogenesis is a continuous process and testis never reach the regressing condition (Pavlov et al., 2009). Nevertheless, this is not exactly the case of *P. pollachius* since a relatively high proportion of regressing males were found just at the end of the spawning season. This is an evidence of ending of the spermatogenesis.

The highest levels of follicular atresia in females were found at the end of the spawning season, a typical feature of species
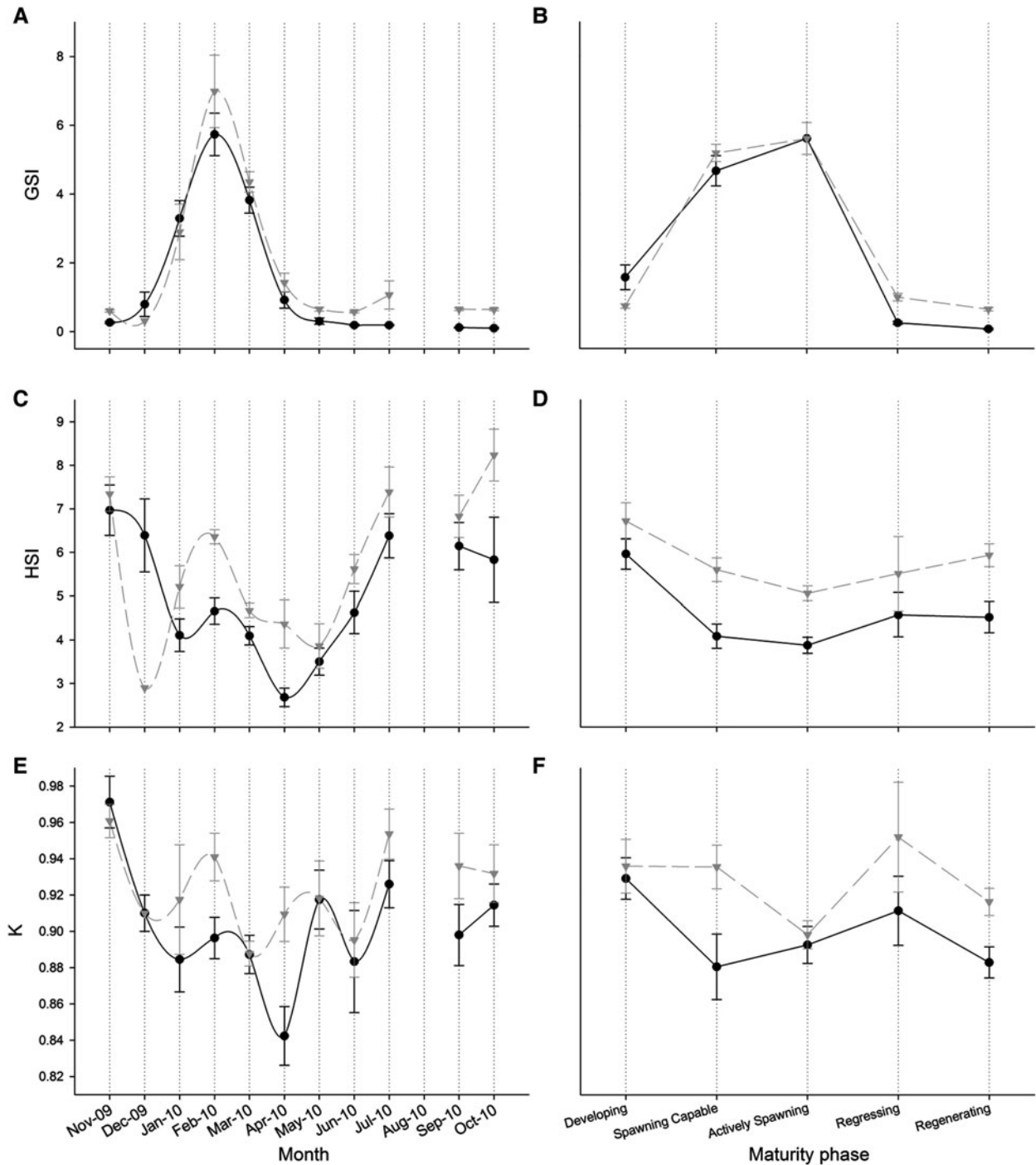
Fig. 7. Sex-specific monthly and reproductive phases variation of somatic indices of *Pollachius pollachius*: (A) GSI vs month; (B) GSI vs reproductive phase; (C) HSI vs month; (D) HSI vs reproductive phase; (E) K vs month; and (F) K vs reproductive phase. GSI, gonadosomatic index; HIS, hepatosomoatic index; K, condition factor. Grey triangles and dashed lines represent females and black dots and solid line represent males. *X* axis labels indicate month and year of sampling.

with asynchronous development of secondary growth follicles (Murua & Saborido-Rey, 2003). Thus, the annual peak of prevalence of atresia seems to mark the end of the female spawning season in the population. This is concurrent with maximum levels of atresia in the regressing females, i.e. resorption of unreleased oocytes (Pavlov *et al.*, 2009).

In ecological studies and in fishery science, body condition factor is widely used to account for the energy reserves stored within individual fish (Marshall *et al.*, 1999). In some temperate species, condition factor fluctuates throughout the year

with no clear seasonal pattern (Méndez & González, 1997; Domínguez-Petit *et al.*, 2010). In the case of *P. pollachius*, the values observed along the year were quite variable but an increase was evident by the end of the spawning season in the values of HSI and K, likely related to active feeding during resting period. Population asynchronicity in spawning activity may make difficult the ecological study of the dynamic of energy allocation and mobilization in a temporal basis (Domínguez-Petit *et al.*, 2010). Therefore, it was deemed convenient to analyse condition factor based on female

Table 3. Variation of somatic indices in relation to reproductive phase of *Pollachius pollachius* from the western coast of Galicia. Summary of multiple generalized least squares (GLS). GSI, gonadosomatic index; HIS, hepatosomoatic index; K, condition factor. Note that the symbol ':' denotes interaction and df means degrees of freedom.

Index		df	F value	P value
GSI	Intercept	1	1313.77	<.0001
$N = 316$	maturity phase	4	113.29	<.0001
$r^2 = 0.65$	sex	1	283.87	<.0001
	maturity phase:sex	4	4.84	0.0009
HSI	Intercept	1	2759.28	<.0001
$N = 317$	maturity phase	4	11.51	<.0001
$r^2 = 0.13$	sex	1	54.44	<.0001
	maturity phase:sex	–	–	–
K	Intercept	1		
$N = 317$	maturity phase	4	2.76	0.0278
$r^2 = 0.05$	sex	1	7.59	0.0062
	maturity phase:sex	–	–	–

Table 4. Sex-specific and sex-combined maturity ogives of *Pollachius pollachius* from the western coast of Galicia. Summary of multiple generalized linear models (GLM). Also, $L_{50\%}$ estimation with correspondent bootstrap uncertainty parameters are provided for females, males and sexes combined.

GLM Coefficients	Estimate	Std Error	Z value	P value
Intercept	−8.70312	0.93227	−9.335	<0.0001
Length	0.24113	0.02346	10.276	<0.0001
Sex(female)	−2.62855	0.49029	−5.361	<0.0001

| Bootstrap $L_{50\%}$ estimates	Original	Bias	Std Error	95% C.I.
Female	46.99	0.026	0.885	45.11 − 48.51
Male	36.09	0.045	1.393	33.06 − 38.66
Combined	42.28	−0.012	0.917	40.46 − 44.10

reproductive phases, rather than based on a temporal pattern. In our study, only HSI followed a clear pattern of variation along the reproductive phases in females and males. This may be related to the role of the liver as a deposit of lipids and glycogen. Actually, the lowest HSI values were observed in individuals with fully developed gonads (actively spawning) whereas females with gonads at the beginning of the developmental process (developing) presented the highest values. This pattern may reflect the cycle of energy reserves and its relationship with gonad development and reproductive

activity. The importance of liver lipid reserves in reproductive activity has also been described in other gadoid species such as *G. morhua* or *T. luscus* (Marshall *et al.*, 1999; Alonso-Fernández & Saborido-Rey, 2012). In the case of *P. pollachius* additional effort is required to properly investigate the energy allocation strategy with biochemical data to better understand the relationship between energy reserves and reproduction.

Age/size at maturity is the most common and well-studied life history parameter in fish exploited populations (Trippel, 1995; Morgan, 2008), as it is used to inform on several stock assessment methods to get a better estimation of limit reference points. Traditionally, estimates of spawning stock biomass (SSB) assumed that all fish mature at the same age
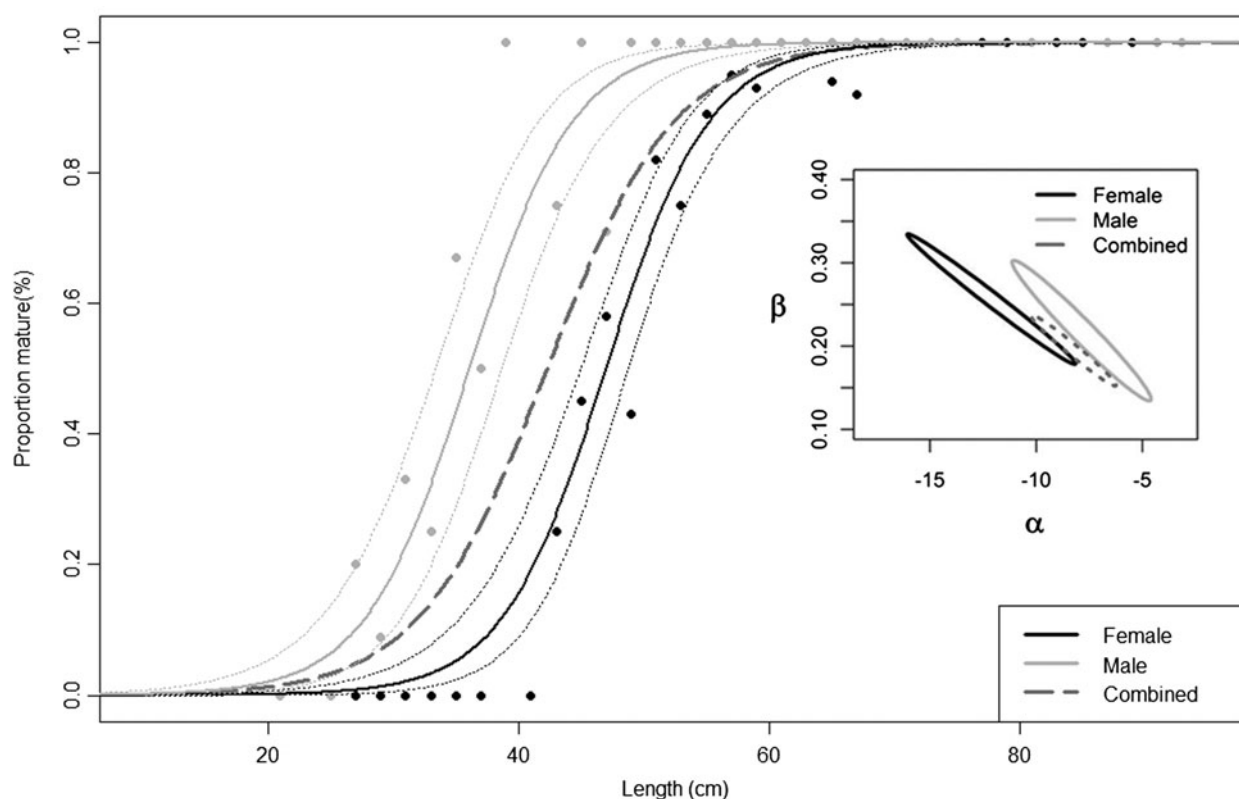
Fig. 8. Sex-specific and sex-combined plots of maturity ogives for *Pollachius pollachius*. The 95% confidence elliptic regions for α (intercept) and β (slope) estimations are shown in the secondary panel.

or use a single invariant maturity ogive (Morgan, 2008). However, the present study estimated significantly different $L_{50\%}$ for females (47.1 cm) and males (36.1 cm). Not considering these differences in future SSB estimations may have important consequences from a quantitative perspective (Morgan, 2008). In a previous study with captive individuals, Omnes *et al.* (2002) estimated an age at maturity of two years (around 0.7 kg) and three years (around 1.1 kg) for males and females, respectively. Although these previous studies were limited in sample size and captivity conditions are not comparable with wild conditions (i.e. continuous feeding in captivity), our results present similar trend especially for females (values in weight obtained from length–weight relationships, see Supplementary Material). $L_{50\%}$ is known to be a highly plastic parameter that changes under external pressure, due to anthropogenic or environmental factors (Trippel, 1995; Domínguez-Petit *et al.*, 2008). Shifts in maturation at smaller sizes and younger ages can have important consequences on stock reproductive potential, affecting egg production (Kraus *et al.*, 2002) and egg and larval viability (Trippel *et al.*, 1997a). However, a long maturation data set is required to detect and validate those changes at a population level. To our knowledge there is no historical maturity data set available for *P. pollachius* in any stock. Worryingly, for a related exploited species such as *P. virens*, a dramatic decrease in $L_{50\%}$ of 16 cm for females and 9 cm for males was recorded in less than two decades in the NW Atlantic (Trippel *et al.*, 1997b). Therefore, we strongly recommend monitoring this parameter to significantly improve the estimation of stock reproductive potential and its integration in stock assessment.

The present study sets the first reproductive knowledge for *P. pollachius* in Galician waters. This information will provide a baseline to improve the reproductive potential estimations and to assess the stock status. Further research should be focused on egg production estimations and age-based demographic analysis to complement present information and provide a better proxy of stock productivity.

Supplementary material and methods

The following supplementary material, referred to in this paper, can be found online at journals.cambridge.org/mbi: length–weight relationships of (A) male and (B) female *Pollachius pollachius* from the present study sampling. Total weight is represented by TW (in g) and total length by TL (in cm).

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