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Reproductive strategy and fecundity of meagre *Argyrosomus regius* Asso, 1801 (Pisces: Sciaenidae): implications for restocking programs

MARÍA DEL MAR GIL [1,3], AMALIA GRAU [1], GUALTIERO BASILONE [2], ROSALIA FERRERI [2] and MIGUEL PALMER [3]

[1] Laboratori d'Investigacions Marines i Aqüicultura, LIMIA (Balearic Government), C/ Eng. Gabriel Roca 69, 07157 Port d'Andratx, Balearic Islands, Spain. E-mail: mmgil@dgpesca.caib.es
[2] Istituto per l'Ambiente Marino Costiero (IAMC-CNR) U.O. di Torretta Granitola, Torretta Granitola, fraz. di Campobello di Mazara (TP), Italy.
[3] IMEDEA-Instituto Mediterráneo de Estudios Avanzados (CSIC-UIB), Department of Ecology and Marine Resources, Ichthyology Group, C/ Miquel Marquès 21, 07190 Esporles, Balearic Islands, Spain.

SUMMARY: Because the meagre (*Argyrosomus regius*) is not currently found around the Balearic Islands (western Mediterranean), the Balearic government is carrying out a restocking programme to recover its population. The success of this programme is critically dependent on improved knowledge of the meagre's life cycle, and particularly its reproductive biology. Data on key reproductive parameters based on both reared and wild specimens are reported here. Histological examinations and gonadosomatic indices from 342 reared specimens demonstrated that 1) the potential reproductive season ranged from April to June and peaked in May, and 2) length at maturity (L_{50}) was 49.3 cm for males and 57.2 cm for females, age at maturity (A_{50}) was 2.7 years for males and 3.5 years for females, and weight at maturity (W_{50}) was 1396 g for males and 1892 g for females. Histological examinations of 37 wild fish from Cádiz (SW Spain) demonstrated that the meagre has determinate fecundity. The annual potential fecundity of reared females ranged from 0.9 to 4.2 million oocytes, which is exponentially dependent upon female size.

Keywords: *Argyrosomus regius*, length at maturity, age at maturity, reproductive season, potential fecundity, Mediterranean Sea.

RESUMEN: Estrategia reproductiva y fecundidad en corvinas *Argyrosomus regius* Asso, 1801 (Pisces: Sciaenidae): Implicaciones en programas de repoblación. – La corvina (*Argyrosomus regius*) actualmente no se encuentra en las Islas Baleares (Mediterráneo Occidental) y, por tanto, se están realizando esfuerzos para recuperar su población a través de un programa de repoblación que se está llevando a cabo por el Gobierno Balear. El éxito del programa de recuperación depende fundamentalmente de la mejora de los conocimientos del ciclo de vida de la corvina, y en particular de su biología reproductiva. Este estudio presenta datos sobre los principales parámetros reproductivos de la especie, basándose tanto en ejemplares criados en cautividad como salvajes. Los exámenes histológicos e índices gonadosomáticos de 342 especímenes criados en cautividad demostraron lo siguiente: 1) la potencial época de puesta se extendió de abril a junio y alcanzó su punto máximo en mayo, y 2) la talla de madurez (L_{50}) fue de 49.3 cm para los machos y 57.2 cm para las hembras, la edad de madurez (A_{50}) fue de 2.7 años para los machos y 3.5 años para las hembras, y el peso de madurez (W_{50}) fue de 1396 g para los machos y 1892 g para las hembras. Los exámenes histológicos de 37 peces salvajes procedentes de Cádiz (SO de España) demostraron que la corvina tiene fecundidad determinada. La fecundidad potencial anual de las hembras criadas en cautividad, la cual está exponencialmente relacionada con el tamaño de la hembra, osciló entre 0.9 y 4.2 millones de ovocitos.

Palabras clave: *Argyrosomus regius*, talla de madurez, edad de madurez, época reproductiva, fecundidad potencial, mar Mediterráneo.

INTRODUCTION

The meagre (*Argyrosomus regius* (Asso, 1801)) is distributed along the Atlantic coast (northward to southern Norway and southward to the Congo), including the entire Mediterranean Sea (Chao 1986). Juveniles (year-round) and adults (during the spawning season) are common in estuarine and shallow coastal areas (Chao 1986, Quéro and Vayne 1987, Quéro 1989), while adults move offshore during the non-reproductive season (Morales-Nin *et al.* 2012). This sciaenid is a highly prized species that is targeted by recreational and commercial fleets (Morales-Nin *et al.* 2010).

Average world catches of meagre were 4408 t year^{-1} from 2005 to 2007 (FAO, 2007), but the real volume of landings is most likely greater because the FAO data for some countries are likely to be underestimated (González-Quirós *et al.* 2011). In Spain, this species is mainly captured by the artisanal (small-scale) fleet, purse-seiners and bottom trawlers. There is only one active commercial fishery, which is located in Cádiz Bay (SW Spain). The average landings are 159 t year^{-1}. Overfishing is likely to occur there (González-Quirós *et al.* 2011).

Sciaenids are prone to overfishing worldwide (Piner and Jones 2004, Silberschneider *et al.* 2009). The high vulnerability of sciaenids has been related to both their large sizes and their aggregating behaviours (in and around estuaries during spawning, Quéro and Vayne 1987). In addition, most sciaenids make sounds that cause spawning aggregations and, consequently, they are easily found and captured (Sadovy and Cheung 2003). Because of its fast growth and high fecundity, the meagre should be a resilient species, but it may in fact be a threatened species (Baldó and Drake 2002, Catalán *et al.* 2006, Lagardére and Mariant 2006, González-Quirós *et al.* 2011).

In Mediterranean waters, meagre populations have suffered alarming declines (Quéro and Vayne 1987) and have disappeared from some areas, such as the Balearic Islands, where they are considered to be critically endangered (Mayol *et al.* 2000). Therefore, a recovery programme has been enforced by the Balearic government. Over 10000 tagged juveniles have been released since 2008 (Morales-Nin *et al.* 2010).

The first requirement for an objective evaluation of the pros and cons of stock enhancement or recovery is the existence of accurate information regarding the ecologic and economic cost-effectiveness of the stocking programme (Born *et al.* 2004). Some factors affecting cost-effectiveness are well known. For example, the somatic growth, feeding and larval survival of meagre have been described (Piccolo *et al.* 2008, Chatzifotis *et al.* 2010, Estévez *et al.* 2010, Roo *et al.* 2010) because of its commercial interest and it has been shown to be a feasible candidate for the diversification of finfish marine aquaculture (Quéméner 2002, Jiménez *et al.* 2005).

The above information raises concern regarding the status of meagre stocks worldwide, exacerbated by the lack of basic biological information on which to base management rules. For example, it is not listed on the Red List of endangered species by the International Union for Conservation of Nature (IUCN) because the available data are too scarce. Knowledge regarding other aspects that are related to meagre life history is insufficient and fragmentary. Specifically, there is a significant knowledge gap in information pertaining to reproductive characteristics, which are key factors for the success of any restocking programme. In addition to their relevance to the success of restocking itself, descriptions of the spawning patterns and reproductive strategies are basic prerequisites for the establishment of suitable management measures (Marshall *et al.* 2003, Joaquim *et al.* 2008, Butler and Rowland 2009, Reñones *et al.* 2010) and for improving culturing practices (Carrillo *et al.* 1995, Cerqueira 2002, Maldonado-García *et al.* 2005). Accurate information regarding sex ratios, reproductive cycles, ages and sizes at maturation and fecundity is lacking in spite of the fundamental roles of these factors in determining the reproductive potential and spawning pattern of any species (Coleman *et al.* 1996, Trippel 1999).

Therefore, the specific objectives here were 1) to describe the reproductive strategy (characteristics of gonad development and reproductive cycle) through histological analyses and biological indices, 2) to determine the age, size and weight at sexual maturation, and 3) to estimate the fecundity of meagre reared in the Balearic Islands.

MATERIALS AND METHODS

Sampling

A total of 342 specimens of meagre were examined in this study. These fish were born (2006, 2007 and 2008) and reared with the techniques developed at the Laboratori d'Investigacions Marines i Aqüicultura installations (LIMIA, Balearic Government, western Mediterranean). Reproduction was based on the hormonal induction of meagre breeders that were captured from Cádiz Bay (Grau *et al.* 2007). The specimens remained under controlled conditions in sea cages (5.5 m diameter) at low density and were fed with commercial feed pellets (Skretting, Burgos, Spain; Grau *et al.* 2007). Sampling periodicity of reared meagre (Table 1) was more frequent during the reproductive season, which has been reported for this species in other areas (Quéro 1989, González-Quirós *et al.* 2011).

The reared meagre exhibits reproductive dysfunction when maintained in captivity (Zohar and Mylonas 2001) because females fail to undergo final oocyte maturation. Namely, final maturation and the spawning of viable oocytes can only be achieved by hormonal induction (Grau *et al.* 2007, Duncan *et al.* 2012). Therefore, 37 wild females from the Gulf of Cádiz (Table 2) were sampled to determine the type of fecundity for meagre (determinate versus indeterminate).

TABLE 1. – List of reared meagre specimens that were used in the present study and macroscopically sexed; I, intermidiate; F, female; M, male.

Date	Birth data	Specimens I	Specimens F	Specimens M	Age (months)	Range of length (cm)
Feb. 2007	2006	10			9	17.7-34.7
Mar. 2007	2006	10			10	20.1-34.8
Nov. 2007	2006	9	16	5	18	35.8-52.3
Feb. 2008	2007	27	3		9	18.9-55.0
May. 2008	2006	10	2	3	24	37.5-60.5
	2007	15			12	21-28.6
Oct. 2008	2007	19	1		17	29.3-35.4
Dec. 2008	2006		4	6	31	52.8-60.5
Apr. 2009	2006		5	5	35	51.3-64.8
May. 2009	2006	1	3	6	36	50-64.3
	2007		10	15	24	31.5-41
	2008	9			12	15.7-26.7
Jun. 2009	2006		2	3	37	52.2-67.5
Nov. 2009	2006		3	2	42	53.1-68
Apr. 2010	2006		5	5	47	50.4-66.3
May. 2010	2006	1	3	6	48	50.3-69
Jun. 2010	2006		3	7	49	60.5-68
Nov. 2010	2008		2	3	30	49.7-56
Dec. 2010	2006		6	4	55	58-79
	2008		2	3	31	52-57.4
Jan. 2011	2007		5	3	44	56.8-70.5
Mar. 2011	2006		6	4	58	63-81.8
Apr. 2011	2007		4	6	47	49.3-68.3
	2006		5	5	59	67.5-78.8
May. 2011	2007		5	5	48	61.8-72.1
	2006		3	7	60	61.6-80.1
Jun. 2011	2007		6	4	49	61.4-70.6
	2006		4	6	61	65.7-84
Jul. 2011	2006		8	2	62	66.8-83.8
Total		111	116	115		

TABLE 2. – List of wild meagre females that were used in the present study.

Date	Specimens	Length (cm)	Fishing gear
Apr. 2006	3	103-166	Trammel net
May 2006	2	120-124	Longline
May 2006	12	114-139	Trammel net
Jun. 2006	4	113-137	Trammel net
Jul. 2006	1	131	Trammel net
Jun. 2007	9	115-151	Trammel net
Jul. 2007	5	132-172	Trammel net
Aug. 2007	1	108	Trammel net
Total	37		

The total lengths (L) of the fish were measured to an accuracy of 0.1 cm and total and somatic body weights (W_T and W_S) to an accuracy of 0.1 g. Then, they were dissected and sexed by visual macroscopic inspection. The gonads and liver were weighed (W_G and W_L) to an accuracy of 0.01 g, and the gonads were preserved in 10% buffered formalin for histological observations.

Sex-related biometric differences

The size differences between males and females were analysed in the oldest specimens (61-62 months old) using ANOVA. A chi-squared test was also performed to determine whether sex ratios differed from the expected proportion of 1:1. These analyses were performed using the SPSS for Windows software (Version 15.0, SPSS, Chicago, IL, USA).

Description of gonad development

The histological preparations of the gonad samples were carried out at IAMC-CNR of Capo Granitola (Italy). Anterior, middle and posterior portions of the gonads were embedded in paraffin with an automatic tissue-processing system (LEICA), sectioned at 3-4 µm and stained with Mayer's haematoxylin and eosin according to the protocol for routine microscopic examination (Luna 1968). Gonads were microscopically sexed, characterized visually and classified at seven different maturity stages for females and eight for males (Table 3; Figs 2 and 3) according to a modification of the microscopic classification that was proposed by Grau *et al.* (2009) and Reñones *et al.* (2010). The histological description of gonad development was carried out with the terminology used by Grau *et al.* (1996 and 2009). The staging of maturity in females was based on the most advanced oocyte developmental stage, the occurrence of atretic vitellogenic oocytes (AO) and the amount of lamellar stroma. The staging of maturity in males was based on male germ cell development and the presence of spermatozoa in the lumens of lobules and/or in sperm sinuses (Reñones *et al.* 2010).

Immature gonads (stage I and II) ranged macroscopically from transparent (stage I; Fig. 2a, b) to translucent (stage II), slender, thread-like structures that were attached to the gas bladders, and they were observed during all seasons in the young specimens. It is not possible to determine sex at this stage by macroscopic inspection. Histologically, females were considered to be immature when only primary oocytes were present, and there was no evidence of prior maturation activity (thick ovary wall). The difference between stage II and stage VII in females (Fig. 3c)

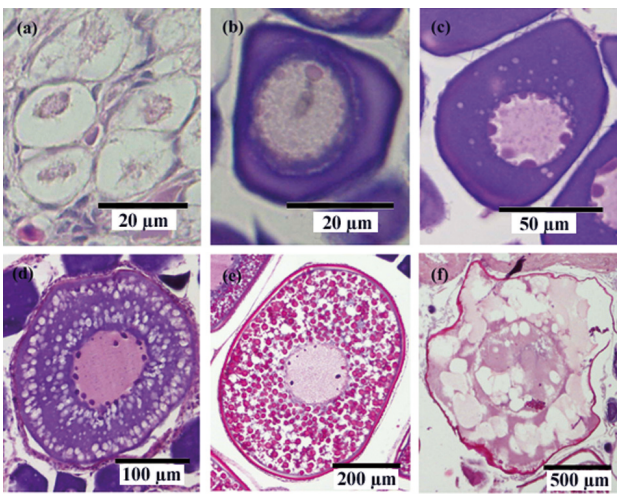

FIG. 1. – Histological observations of oocytes of meagre: a) Oogonia. b) Chromatin-nucleolus. c) Perinucleolar oocyte. d) Cortical alveoli oocyte. e) Secondary vitellogenic oocyte. f) Hydrated oocyte.

TABLE 3. – Microscopic maturity classification criteria for ovaries and testes of meagre.

Stage	Ovary	Testis
IMMATURE STAGES		
I. Incompletely differentiated	Wide ovarian cavity. Cortical region contains numerous oogonia (Fig. 1a, 2a) and some primary oocytes, both chromatin-nucleolus (Fig. 1b) and perinucleolar oocytes (Fig. 1c).	Testes lack a well-defined tubular system with numerous spermatogonia (Fig. 2b).
II. Differentiated immature	Developed and packed lamellae with abundant oogonia and primary oocytes, mainly perinucleolar oocytes.	Testes well-developed with numerous tubules filled with spermatogonia. Some spermatogenic cysts can be observed in all developmental stages, even spermatozoa can be observed during reproductive season.
MATURE STAGES		
III. Developing	Numerous primary oocytes and very few oogonia. Presence of cortical alveolar oocytes (Fig. 1d).	Spermatogenic activity is widespread throughout the testis. Some spermatogonia are observed on the edge of the gonad. Few spermatozoa can be observed in some tubules when the testes are in the first maturation stage. Otherwise, some free residual spermatozoa are observed in some tubules and vas deferens from the last reproductive period.
IV. Ripening	Gonads are enlarged and contain secondary vitellogenic oocytes (Fig. 1e). Further stages of oocyte growth (final oocyte maturation) have not been observed and levels of atresia increase during the season but remain low (<30% vitellogenic oocytes). Very few oogonia and some primary and cortical alveolar oocytes can be observed (Fig. 2c). Post-ovulatory follicles (POF) are not detected.	Tubules filled with spermatogenic cysts in all developmental stages. Abundant spermatozoa are observed in many but not all of the tubules (Fig. 2d).
V. Running	Not observed in captive conditions, just in wild specimens (Fig. 1f).	Spermatogenic activity is intense. Numerous spermatozoa in the large lumen of all tubules and vas deferens (Fig. 3a).
VI. Spent	Massive levels of atresia are detected at this stage (>30% vitellogenic oocytes). Only some healthy and resting primary oocytes can be observed (Fig. 3b).	Numerous spermatozoa in all tubules and vas deferens. Spermatogenic activity is very limited or non-existent.
VII. Recovering	Abundant oogonia and primary oocytes. Ovary is bigger in diameter and ovary wall is thicker than those of differentiated immature ovaries. Many large MMC and MB are present along the axis of the ovigerous lamella (Fig. 3c).	Abundant free residual spermatozoa in the tubules and vas deferens. Numerous spermatogonia cover all spermatogenic tubules.
VIII. Resting	Not observed.	Numerous spermatogonia and some spermatogenic activity are beginning on walls. Some free residual spermatozoa are observed in some tubules and vas deferens (Fig. 3d).

was established according to a combination of criteria that determine prior maturation activity, including a thick tunica albuginea, the presence of muscle bundles (MB), and the presence of melano-macrophage centres (MMC), which result from the resorption processes of the atretic oocytes in mature females. These criteria have been applied in other species, e.g. *Epinephelus marginatus* (Marino *et al.* 2001, Reñones *et al.* 2010) and *Synbranchus marmoratus* (Ravaglia and Maggese 2002). The presence of MB has been widely employed as a diagnostic criterion of prior maturation (Shapiro *et al.* 1993, Sadovy and Colin 1995, Fennessy 2006, Pears *et al.* 2006, Reñones *et al.* 2010).

Reproductive cycle

The potential reproductive period in captivity was determined by analysing the seasonal (monthly) evolution of the percentage of reared individuals at different mature stages listed in Table 3, and three biological indices that are related to reproduction: the gonadosomatic (I_G), hepatosomatic (I_H) and condition (K) indices, which were estimated using the following equations:

$$I_G = W_G\ 100\ W_S^{-1}$$
$$I_H = W_L\ 100\ W_S^{-1}$$
$$K = W_S\ L^{-3}$$

where W_G is the gonad weight (g), W_L is the liver weight (g), W_S is the somatic weight (g) and L is the total length (cm).

Biological condition (welfare) may be estimated using a number of different indices, and the selection of the most proper index is species-specific and depends on growth (Bolger and Connolly 1989). Fulton's index

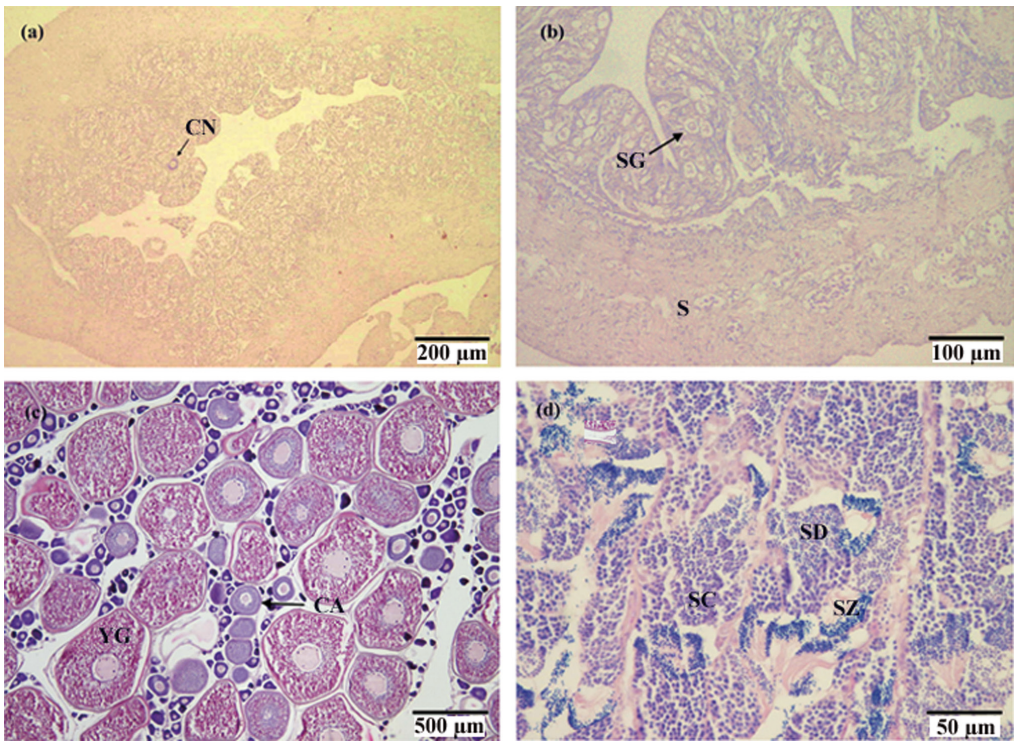

FIG. 2. – Sections of female and male meagre gonads. a) Immature ovary (Stage I) with abundant oogonia and some previtellogenic oocytes (chromatin-nucleolus (CN) and perinucleolar stages). b) Immature testis (Stage I) with abundant stroma (S) and numerous spermatogonia (SG). c) Ripening ovary (Stage IV), vitellogenic oocytes at cortical alveoli (CA) and yolk granule (YG) stages are present. d) Testis at ripening stage (Stage IV) with intense spermatogenic activity: abundant spermatocytes (SC), spermatids (SD) and spermatozoa (SZ).

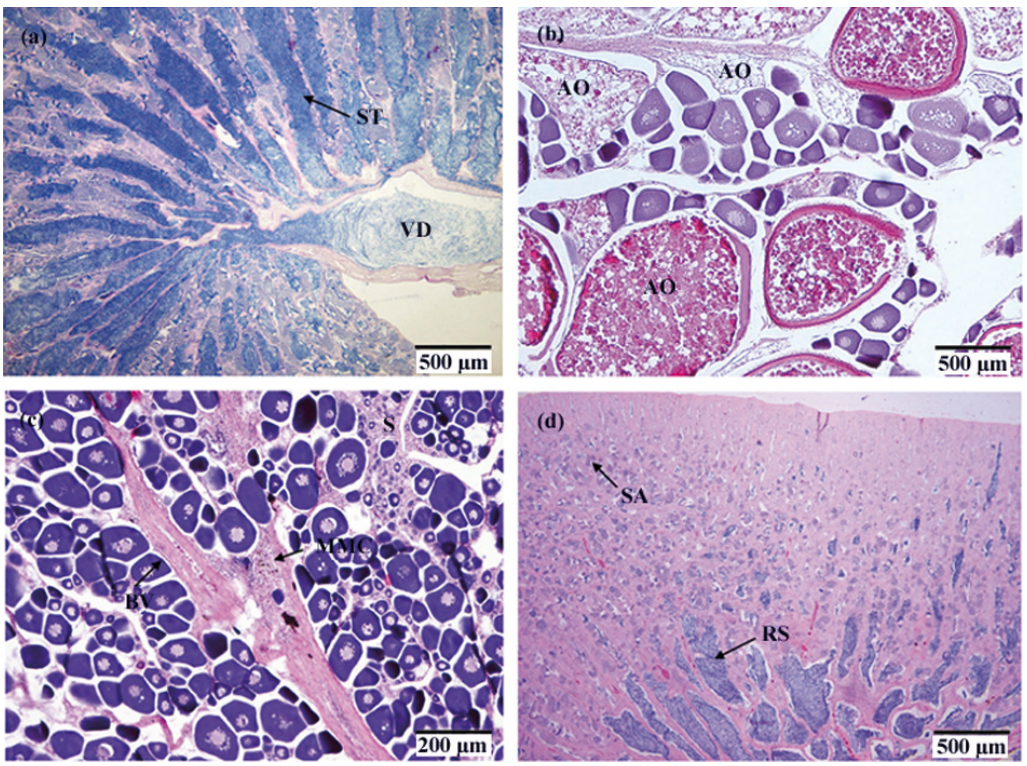

FIG. 3. – Sections of female and male meagre gonads. a) Running testis (Stage V) with spermatogenic tubules (ST) and vas deferens (VD) filled with spermatozoa. b) Spent ovary (Stage VI) with numerous atretic vitellogenic oocytes (AO) at different levels of degeneration. c) Recovering ovary (stage VII), showing abundant stroma (S), melanomacrophage centres (MMC) and muscle bundles (MB) around blood vessels. d) Resting testis (Stage VIII); spermatogenic activity (SA) is beginning and residual spermatozoa (RS) remain in some tubules.

(K) is recommended when the relationship between size and weight is $W=aL^3$ (Bolger and Connolly 1989, Basilone *et al.* 2006). The value of the exponent was tested (t test) to determine whether it differed significantly from 3.

The existence of between-month differences in the three biological indices was tested using ANOVA. Post-hoc pairwise comparisons were completed using Tukey's test. These analyses were performed using the SPSS for Windows software (Version 15.0, SPSS, Chicago, IL, USA).

Maturity status

The maturity ogives for females and males were determined by adjusting the proportions of mature specimens to logistic curves in relation to L, which was grouped into 2.5-cm length intervals, age, which was grouped into 5-month increments, and weight, which was grouped into 200-g increments. Length at maturity (L_{50}) was defined here as the length at which 50% of the specimens were mature, age at maturity (A_{50}) as the age at which 50% of the fish were mature, and weight at maturity (W_{50}) as the weight at which 50% of the fish were mature. In the analysis, immature fishes were those with gonads at stage I and II, while mature fishes were made up of grouped individuals with gonads at the remaining stages. For females, the ovaries in stage II (developing immature) and stage VII (recovering) were difficult to differentiate when the fish were outside the reproductive season, which may induce errors in the estimation of L_{50}. To avoid any bias, two ogives were estimated for females (Pears *et al.* 2006): 1) the percentage of all ovaries (n=170), and 2) the percentage of females that were sexually active before and during the reproductive period (n=118). An analysis of the residual sum of squares (Chen *et al.* 1992, Haddon 2001) was applied to compare the logistic curves (Basilone *et al.* 2006). For males, determinations were made using the whole dataset (n=167). The maturity ogives were estimated via an analytical method that was based on a logistic non-linear regression model (Hunter *et al.* 1992, Roa *et al.* 1999):

$$P_L=1\ (1+e^{(\beta_0+\beta_1 L)})^{-1}$$

where P_L is the proportion of mature specimens at size L (age or weight), and β_0 and β_1 are the intercept and slope parameters of the logistic regression between body length (age or weight) and the percentage of mature individuals. Confidence limits of L_{50}, A_{50} and W_{50} were estimated using the method described by Roa *et al.* (1999).

Fecundity

Fecundity type can be determinate (number of eggs that are released during the spawning season is fixed prior to the onset of spawning) or indeterminate (number is not fixed prior to the onset of spawning). The methodology for estimating the potential fecundity (total number of eggs potentially laid per female and spawning season) depends on the type of fecundity (Hunter *et al.* 1992, Murua and Saborido-Rey 2003). The fecundity type for meagre was determined using data from wild females from the Gulf of Cádiz and was used to determine the potential fecundity of both the reared population in the Balearic Islands and the wild population.

The type of fecundity was identified by measuring the following during the spawning season: 1) the oocyte size-frequency distribution, 2) the variation in the proportion of vitellogenic oocytes and 3) the variation in the mean diameters of advanced vitellogenic oocytes (Hunter *et al.* 1992, Murua and Saborido-Rey 2003). These measurements were obtained from six wild females from Cádiz, three at the ripening (stage IV) and three at the running stage (stage V). The oocyte size-frequency estimation included all of the oocytes within the microscopic field using a 4× objective to avoid any bias. Oocyte size was estimated by averaging the maximum and minimum diameters. Only oocytes that had been sectioned through the nucleus were considered (Foucher and Beamish 1980). There was no need to apply a correction factor because the purpose of the cell measurements was only to compare the relative oocyte size-frequency distributions between individuals throughout the spawning season and not to quantify oocyte abundances.

In species with determinate fecundity, such as the meagre (see results), the annual fecundity (number of eggs laid per year) is thought to correspond to the potential annual fecundity (F_P) after correcting for atretic losses. The potential annual fecundity is defined as the number of developing oocytes ([NDO], cortical alveoli and vitellogenic oocytes) per female in a reproductive season with no correction for atretic losses (Hunter *et al.* 1992). The NDO was estimated by the gravimetric method. A subsample of 0.050 g was filtered through a 150-μm mesh to eliminate previtellogenic oocytes, so only cortical alveoli and vitellogenic oocytes were manually counted. The F_P was estimated in the ovaries at the ripening stage (stage IV, Table 3); however, in the case of reared meagre, only those ovaries that had not begun to show atresia were analysed because they do not release eggs, and batches of oocytes become atretic and reabsorbed. Therefore, six reared females ranging in size from 49.3 to 78.2 cm and eight wild individuals from 104 to 166 cm were used for the estimation of the F_P. The existence of differences in the F_P between the reared and wild females was evaluated using an analysis of covariance (ANCOVA). Fish weight was included as a covariable because, as in other species, the F_P is related to fish biomass (Marshall *et al.* 2003). This statistical analysis was completed with R (Version 2.14.0, http://www.r-project.org/).

RESULTS

Sex-related biometric differences

The 342 reared meagre ranged from 15.7 to 84 cm for *L*, 31.6 to 7110 g for total weight (W_T) and were from 9 to 62 months for age. Females (n=173) ranged from 15.7 to 83.8 cm for *L* and 31.6 to 6523 g for W_T. Males (n=169) ranged from 17.7 to 84 cm for *L* and 58.9 to 7110 g for W_T. The oldest specimens (61-62 months old, n=20) showed no differences in length between the sexes ($F_{1, 18}$=0.014; P=0.907). The observed sex ratio (1:1.02 male:female) did not differ significantly from the expected proportion (χ^2=0.047, d.f.=1, P>0.05).

Description of gonad development

The gonads of the meagre were longitudinal, paired and fused at their last caudal portions and the short oviducts leading into the urogenital pore, which were posterior and clearly differentiated from the anus. The gonads, which were similar in length, were attached to the ventral walls of the gas bladders and suspended by mesenteries to the dorsal walls of the body cavities. The testes were oval or triangular in section, lobular in structure and white in colour except in the spent period, when the colour was greyer. The ovaries were circular in section and orange in colour and changed to redder or browner during the spent period.

No histological differences were detected between the development of the anterior, middle and posterior subsamples of the gonads. The gonad study, based on the histological examinations, confirmed that the meagre is a gonochoristic species that exhibits an asynchronous ovarian developmental organization; i.e. oocytes at all stages of development are present without a dominant population (Murua and Saborido-Rey 2003), and it is a serial batch spawner.

Reproductive cycle

The monthly pattern (Fig. 4) that is depicted by the results of the histological analyses agrees with the seasonal variability in I_G (Fig. 5). The seasonal (monthly) variations of reared meagre (Fig. 4a, b) indicate that the reproductive cycle of the species is asynchronous at the population level, i.e. not all the individuals are at the same gonad development stage at the same time (Reñones *et al.* 2010). In both sexes, gonads at the initial developmental stages were observed for the first time in January. Ripening females were observed from April to June, while running males were found from March to June. The peak of the running stage occurred in males in April (93%) and May (81%); during these months, the percentages of ripening females were 60% and 100%, respectively. The percentage of ripening females and running males declined in June, which is when the proportions of spent gonads increased (47% of males and 58% of females). The proportion of females at the recovery stage increased from June until December (100%). The absence of resting females in

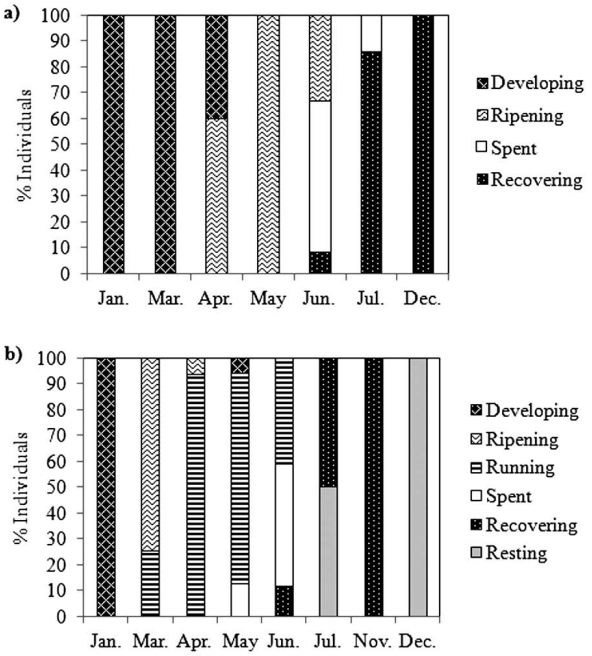

FIG. 4. – Monthly evolution of percentage of mature gonads for each stage for (a) females (n=53) and (b) males (n=62) of meagre.

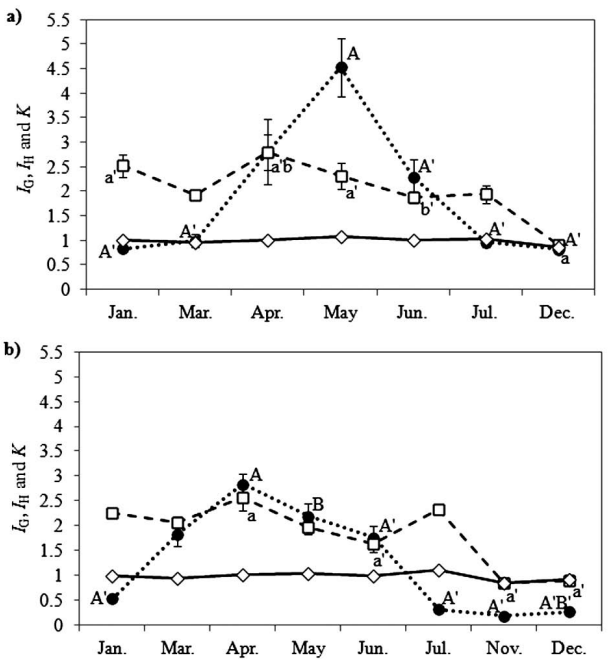

FIG. 5. – Trends of gonadosomatic index (I_G, ●), hepatosomatic index (I_H, □) and condition factor (K, ◊) for (a) females and (b) males. Standard error of the mean is represented by vertical bars. The statistically diferent pairwise comparations were represented with the same letter (e.g. in the I_G of females, April (A) was significantly diferent from January, March, June, July and December (A')). Uppercase letters were used for the I_G and lowercase letters were used for the I_H. K values did not differ significantly between months in either of the two sexes.

TABLE 4. – Gonadosomatic (I_G), hepatosomatic (I_H) and condition (K) indices for the gonad stages (mean±standard error), and ANOVA analyses results (F-value).

Stage	Female			Male		
	I_G	I_H	K	I_G	I_H	K
Developing	0.87±0.048	1.96±0.110	0.96±0.014	0.29±0.073	1.95±0.241	0.99±0.023
Ripening	3.58±0.417	2.53±0.212	1.04±0.020	1.45±0.242	1.98±0.243	0.98±0.018
Running				2.31±0.141	2.06±0.114	1.03±0.012
Spent	2.67±0.455	2.00±0.182	0.98±0.014	1.44±0.228	1.53±0.182	0.98±0.029
Recovering	0.84±0.037	1.49±0.185	0.98±0.035	0.21±0.030	1.15±0.213	0.86±0.051
Resting				0.25±0.024	1.30±0.278	0.97±0.042
F-value	22.87**	5.49*	3.21*	18.46**	3.27*	4.84**

* Significant (P<0.05), ** Highly significant (P<0.001)

December indicates that the ovaries of meagre recover during the winter and are not active until the next reproductive season. The recovery stage of the testis was observed in June, July and November, and the resting stage increased from July to December (100%).

This pattern is in agreement with the seasonal variability of I_G. The mean I_G values for females were lower than 1 in July and from December to March. Then, I_G increased sharply in April, peaked in May and decreased in June (with I_G>2). I_G was generally higher for females than for males except in March, when the mean I_G value was significantly higher ($F_{1,\ 8}$=11.782; P<0.05) for males. In males, the mean I_G started to increase in January, peaked in April and decreased to the lowest values in July, November and December. Monthly differences in I_G (Fig. 5) were significant for females ($F_{6,47}$=8.896, P<0.001) and males ($F_{7,54}$=7.750; P<0.001). The highest value for female I_H was observed in April, prior to the peak of I_G, after which it decreased gradually during the reproductive season. The same trend was observed in males. Monthly differences in I_H (Fig. 5) were significant for females ($F_{6,47}$=5.357, P<0.001) and males ($F_{7,54}$=3.942, P<0.05). In contrast, K values did not differ significantly between months in either of the two sexes (P>0.05).

The comparison of biological indices measured from fish at different stages of gonad maturity provided additional information (Table 4). I_H differed significantly between fish at different gonad stages in both sexes (females $F_{3,55}$=5.49, P<0.05; males $F_{5,81}$=3.27, P<0.05). The lowest values corresponded to recovering individuals. K differed significantly between developing and ripening stages in females ($F_{3,55}$=3.21, P<0.05). However, in males, significant K differences were observed between running, spent and recovering individuals, with the latter showing the lowest values ($F_{5,81}$=4.84, P<0.001).

Maturity status

The smallest and youngest mature female was 53.5 cm L and 35 months old. The smallest and youngest mature male was 37.5 cm L and 21 months old. The sizes at 50% maturity were estimated to be 49.3 cm L (logistic model 95% C.I.=48.3-50.7 cm) for males and 57.2 cm L (logistic model 95% C.I.=56.3-58.2 cm) for females (Fig. 6). When the two ogives (fitted with all samples and fitted with the samples during the reproductive season) were compared in females, a significant difference in L_{50} was found (F=9.691, P<0.001).

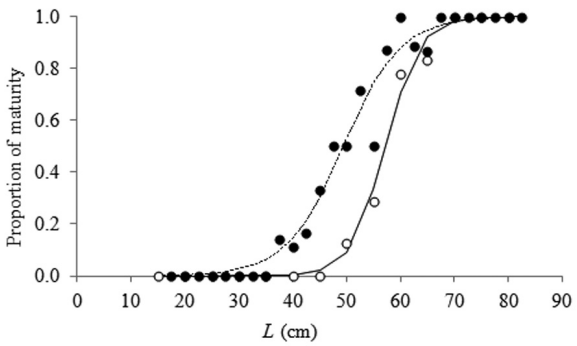

FIG. 6. – Probability curve of maturation of meagre for males (●) and females (O).

The age at 50% maturity (A_{50}) was estimated to be 32.3 months (logistic model 95% C.I.=31.8-32.8 months) for males and 42.1 months (logistic model 95% C.I.=40.4-43.9 months) for females. In addition, the weight at maturity (W_{50}) was 1396 g (logistic model 95% C.I.=1228-1563 g) for males and 1892 g (logistic model 95% C.I.=1754-2029 g) for females.

Fecundity: type and estimates

The histological examinations of the ovaries and their oocyte size-frequency distributions from the wild meagre females allowed the fecundity type to be identified. The numbers of measured oocytes per gonad ranged from 75 to 490 (mean 217±168 sd). Prior to spawning (Fig. 7a), oocytes were present at any stage of development including the vitellogenic (220-620 μm), cortical alveoli (150-210 μm) and primary oocyte (<140 μm) stages. The distribution of oocyte size in a given gonad revealed several well-differentiated modes. The hiatus between the previtellogenic and vitellogenic oocytes was evident. The same pattern was observed at any time during the spawning season. For example, at the end of the spawning season, the oocyte size distribution was multimodal (Fig. 7b) with clear hiatus between batches. The ovaries at the end of the spawning season also showed marked depletions in vitellogenic oocytes and concurrent small amounts of oocyte atresia. The proportion of vitellogenic oocytes

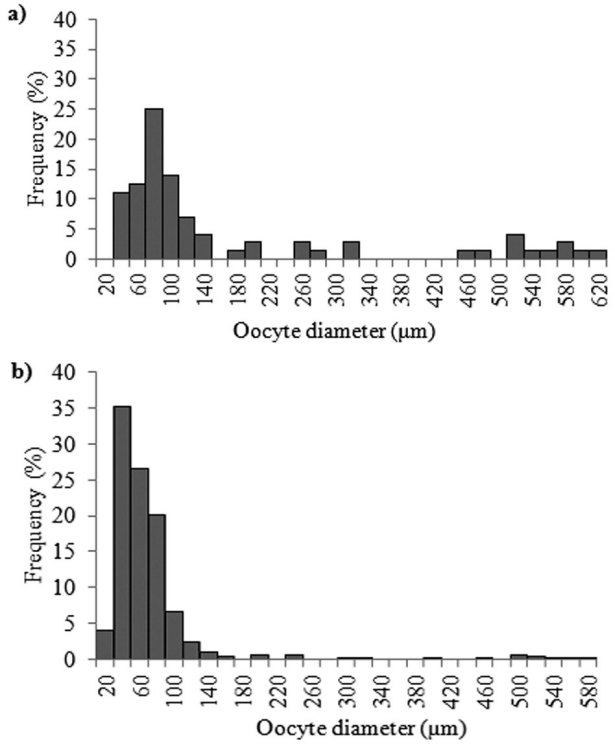

FIG. 7. – Size-frequency distribution of oocyte diameters grouped per 20 μm from histological sections of 2 meagre females. a) 166 cm *L* female captured in April at ripening stage. b) 108 cm *L* female captured in August at final spawning stage.

(>150 μm) decreased significantly ($F_{1,4}$=13.1, P<0.05) throughout the spawning season. However, their mean diameters did not change ($F_{1,5}$=0.3, P>0.05) during the spawning period. All of these factors indicate that the fecundity of meagre is determinate and also confirm that oocyte development is asynchronous.

In reared females (n=6), the F_P ranged from 0.9 to 4.2 million oocytes. Despite this relatively small sample size, the trend observed suggests the existence of a monotonic increase in F_P along with length, weight and age. However, *K* did not seem to have any significant effect on fecundity (Table 5). In wild females, the

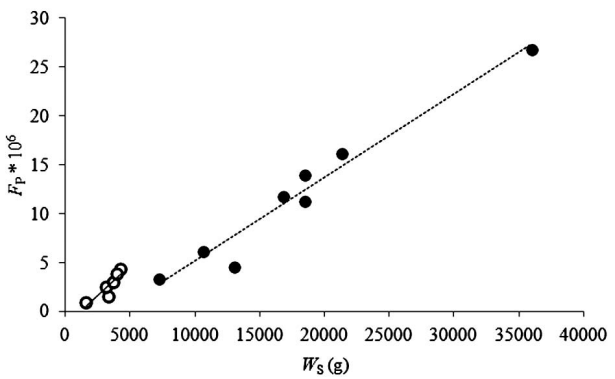

FIG. 8. – Curve of F_P-weight relationship. White circles correspond to reared females, and black circles correspond to Cádiz wild females.

TABLE 5. – Regression analysis for the effects of total length (*L*), somatic weight (W_S), age and condition index (*K*) on potential annual fecundity in ripening reared females.

Fecundity	P	r^2
F_P=0.0686 e $^{0.0511\,L}$	0.04	0.797
F_P=0.0012 W_S–1.434	0.02	0.756
F_P=0.172 Age–6.471	0.02	0.748
F_P=–4.785 *K*+7.565	0.13	0.469

F_P ranged from 2.1 to 31.1 million oocytes. Given the general relationship between F_P and size (and age), the differences between reared and wild populations (Fig. 8) were tested using an ANCOVA. The slopes of the two (reared vs. wild) F_P-W_S regression lines did not differ significantly (interaction group*W_S=–3.6 10^{-4}, P=0.59). However, there were significant differences in intercepts between the reared and wild females ($F_{1,11}$=8.55, P<0.005). These results indicate that the two regression lines were parallel and that for any given W_S, F_P is greater in reared females.

DISCUSSION

The meagre has been the subject of increasing interest. It is a feasible candidate for the diversification of European aquaculture, which has promoted a number of studies regarding the optimization of its aquaculture production (Quéméner 2002, Jiménez *et al.* 2005, Roo *et al.* 2010, Monfort 2010). Additionally, the growing awareness of the conservation status of its wild populations has justified the study of its fisheries and population dynamics (Quéméner 2002, Prista *et al.* 2007, González-Quirós *et al.* 2011).

In the Balearic Islands, the interest is focused on restocking because the species is critically endangered (Mayol *et al.* 2000). The data reported here has important implications for the management of fisheries, aquaculture production and restocking quality control.

With regard to sexual maturation, we recommend the use of samples that have been obtained during the reproductive season for the estimation of maturity ogives because mistakes in the classifications of stage II and VII in females may occur, as shown by the significant differences between the two calculated ogives. In reared meagre, females matured at longer lengths and older ages than males, which is typical of others sciaenids (Griffiths and Hertch 1995, Griffiths 1996, Grau *et al.* 2009, Silberschneider *et al.* 2009). However, the most important result that has been reported here is that the length and age at maturity differed considerably from previous results using wild populations; these values were 61.7 cm *L* for males and ranged from 70 to 110 cm for females (Tixerant 1974, González-Quirós *et al.* 2011). For *A. japonicus*, the length and age at maturity also appear to differ regionally (Silberschneider *et al.* 2009). According to Tormosova (1983), the stock density, food and water temperature may influence the growth and reproductive potential of fish and affect the size and age of first maturity. In fact, these parameters

are known to be highly plastic, so they are subject to change in response to environmental factors or intrapopulation drivers, such as the growth rate or mortality rate (Stearns and Crandall 1984, Wootton 1990, Trippel 1995, Marshall *et al.* 2003, Hamilton *et al.* 2007, Linde *et al.* 2011). It has been evidenced that some fishes mature earlier in captive conditions than in the wild (Zohar *et al.* 1978, Hard *et al.* 1985, Micale *et al.* 2002). The plasticity of reproductive parameters and the increased food availability could explain the early sexual maturation. However, it has been suggested that differences in size (or age) at sexual maturation among wild populations (or between reared and wild populations) may be spurious; selecting sampling according to site or time may result in subsamples that are biased by sexual maturation stages due to differential mortality, differential migration, spatial segregation or selective catching (Sadovy and Shapiro 1987, Micale *et al.* 2002). Nevertheless, when between-locality differences are observed, as in this case, local data should be preferred for the selection of optimal management options (Silberschneider *et al.* 2009). No wild populations remain in the Balearic Islands; therefore, it is advisable to use the data reported here instead of those from distant wild populations.

The sex ratio of the studied reared population of meagre is 1:1, although deviations from this ratio are common in other sciaenids (Fennesy 2000). These deviations in the wild populations of sciaenids may be due to a differential mortality, migration or spatial and temporal segregation between males and females instead of a differential birth rate.

The sampled adults that were 5 years of age (61-62 months old) showed no differences in length between the sexes. The same results have been obtained in the wild population from the Bay of Cádiz (González-Quirós *et al.* 2011) for specimens that were up to 13 years of age. However, other sciaenids show significant between-sex growth differences, with the females growing faster (Griffiths and Hetch 1995, Fennesy 2000, Grau *et al.* 2009, Silberschneider *et al.* 2009). One possible explanation for the growth differences is associated with sex-related maturity differences (Imsland *et al.* 1997). However, growth differences seem to be more related to the fact that the energy spent by males in growth and reproduction is less than that spent by females, indicating the presence of some energy-saving mechanism in males (Imsland *et al.* 1997).

The histological analyses of the gonads showed that the meagre undergoes asynchronous ovarian development, i.e. oocytes from all developmental stages are present, and there is not a single dominant cohort (Murua and Saborido-Rey 2003). This implies that the meagre is a batch spawner, i.e. eggs are released in batches over a relatively protracted period (Mayer *et al.* 1990, Murua and Saborido-Rey 2003). All of the other Sciaenidae that have been studied to date show the same type of ovarian development (Wilson and Nieland 1994, Lowerre-Barbieri *et al.* 1996, Barbaro *et al.* 2002, Macchi *et al.* 2003, Roumillat and Brouwer 2004, Hutchings *et al.* 2006, Yamaguchi *et al.* 2006, Dadzie 2007, Grau *et al.* 2009, Lim *et al.* 2010). However, meagre ovarian development has been qualified as group-synchronous by Duncan *et al.* 2012, although histological examinations were not applied. The meagre has a short period of vitellogenesis. In the reared population from the Balearic Islands, this period begins in April and ends in June. Similar results were reported with captive meagre in Greece (Sigelaki *et al.* 2011). Therefore, reared populations seem to have shorter reproductive seasons than that of the wild South Atlantic population, which extends from late winter to mid-summer (González-Quirós *et al.* 2011). However, the spawning period shows substantial differences between localities: for example, a duration of 15 days in Biscay Bay (Quéro 1989). The potential reproductive season of reared meagre coincides with raising water temperatures (personal unpublished data) and maximum photoperiods (data from Ministerio de Fomento, Spanish government) in the Balearic Islands. During the activity peak of males, the temperature is around 15-16°C and day length is 13 hours, and in the case of females, the temperature is around 17-18°C and day length is 14.2 hours. In these warm months, phyto- and zooplankton productivities are high (Estrada *et al.* 1985, Fernández de Puelles *et al.* 2004, Macpherson and Raventos 2006). Most of the fish species living in temperate waters tend to show the same patterns (examples of fish from the Balearic Islands: Grau *et al.* 2009, Reñones *et al.* 2010). The ripening peak coincides with a peak in I_G, which has often been used to delimit the reproductive season (Wilk *et al.* 1990). The sharp decrease in this index after the peak suggests a quick egg loss without replacement. This is the pattern that is expected in fish with determinate fecundity. However, in the case reported here, reared meagre do not release eggs, as has been observed in other studies (Sigelaki *et al.* 2011, Duncan *et al.* 2012), and their batches undergo atresia and are reabsorbed. This is a common reproductive dysfunction of cultured fishes (Zohar 1989, Mylonas *et al.* 2004).

In many fishes, the I_H and condition indices are inversely associated with the I_G. This pattern is explained by the mobilization of reserves from other tissues to the gonads to supply the energy requirements for reproduction (Merayo 1996, Murua *et al.* 2006, Alonso-Fernández *et al.* 2008). In fishes, such as members of the family Gadidae in whom the liver acts as the main lipid reservoir, mean monthly I_H values exhibit dramatic variations according to the energetic status of the fish that correlate well with I_G variations (Jensen 1979, Lambert and Dutil 1997, Alonso-Fernández *et al.* 2008). However, in this study, I_H showed a peak in April in both sexes prior to the ripening peak and decreased thereafter. Additional evidence of the role of the liver in the energy balance is shown by the differences in I_H that are observed between fish at different maturity stages; recovering fish have the lowest I_H

values in both sexes. Therefore, in meagre, as in other Sciaenidae (Craig *et al.* 2000, Grau *et al.* 2009), the role of the liver as the main lipid reservoir is questionable. Instead, this pattern suggests that the mobilization of energy reserves for gonad development is dependent on the total energy that is stored within the body. In fact, in other Sciaenidae, lipid reserves are found in the liver but also in other reservoirs (Craig *et al.* 2000, Grau *et al.* 2009).

The condition index (*K*) remains nearly constant throughout the year, indicating that the condition of the meagre is not affected by reproductive efforts. Only recovering males and developing females exhibit significantly poorer conditions (*K*). Other sciaenids show the same pattern (Grau *et al.* 2009, Lim *et al.* 2010), but it is not easily extrapolable to wild populations or species because the intensive feeding supply to the farmed meagre could confound the effects of any other environmental factor.

Through studying wild specimens, it was possible to conclude that the fecundity type of meagre is determinate. This was evidenced by the well-developed hiatus between the previtellogenic and vitellogenic oocytes during the spawning period. The decreased percentage of vitellogenic oocytes and the absence of a generalized prevalence of atresia toward the end of spawning provided additional support for the existence of the determinate type of fecundity. However, the diameters of vitellogenic oocytes did not increase over the spawning period, as would be expected in a species with determinate fecundity (Hunter *et al.* 1992); this feature has also been observed in other asynchronous determinate species (Alonso-Fernández *et al.* 2008, Reñones *et al.* 2010). Asynchronous oocyte development is normally associated with an indeterminate fecundity strategy (Murua and Saborido-Rey 2003), but in some species, determinate fecundity is believed to exist despite asynchrony in oocyte recruitment (Murua and Saborido-Rey 2003, Alonso-Fernández *et al.* 2008, Reñones *et al.* 2010).

Meagre, like many other members of the family Sciaenidae, is a highly fecund fish (Sadovy and Cheung 2003). For example, the red drum (*Sciaenops ocellatus*) spawns 20-40 million eggs per season in females with a fork length of 697-1005 mm (Wilson and Nieland 1994) and the black drum (*Pogonias cromis*) spawns between 13-67 millions in females of similar size (Nieland and Wilson 1993). The fecundity reported here ranges from 0.9 to 4.2 million oocytes for the reared females (493-782 mm of total length) and from 2.1 to 31.1 million for the wild females from Cádiz (1040-1660 mm of total length).

The number of potential offspring that meagre females can produce in a reproductive period is influenced by maternal attributes. The potential fecundity of the meagre increased exponentially with size and linearly with weight and age, as is observed in other species (Marshall *et al.* 1998, Lloret and Rätz 2000, Reñones *et al.* 2010). However, the vast differences in size that are considered here cast some doubts on the pattern that was observed because reared females presented higher potential fecundities for a given somatic weight than wild females. Size-independent, between-population variability in fecundity has only been reported recently (Lowerre-Barbieri *et al.* 2009), and it has potential effects on population dynamics; therefore, further investigation of this topic is needed.

The reproductive parameters that are presented here are essential for optimizing the design of the restocking project. For example, a late age at first maturity is disadvantageous for recovering a sustainable wild population (Bell *et al.* 2005). In contrast, the high fecundity of the meagre favours the recruitment of juveniles and therefore the success of the restocking programme. However, this high fecundity may not occur in the released reared meagre. For example, extensive research involving mainly salmonid restocking has revealed the existence of reduced reproductive fitness in the majority of cultured fish that are released into the wild (Fleming and Gross 1993, Fleming *et al.* 1996, Jonsson 1997, Jonsson and Jonsson 2006), which is primarily due to the retention of unspawned eggs. This fact has also been observed in Dover sole (Houghton *et al.* 1985). Furthermore, the percentage of released individuals that survive to reach reproduction capacity can be estimated through the collected recapture data only when the size or age at maturity is known. To date, some restocked mature specimens have been recaptured from the wild (unpublished data), but until now, no evidence of natural spawning has been obtained from the Balearic Sea.

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REFERENCES

Alonso-Fernández A., Dominguez-Petit R., Saborido-Rey F., Bao M., Rivas C. 2008. Spawning pattern and reproductive strategy of female pouting, *Trisopterus luscus* (Linnaeus, 1758), in the Galician shelf (northwest Spain). *Aquat. Liv. Res.* 21: 383-393.

Baldó F., Drake P. 2002. A multivariate approach to the feeding habits of small fishes in the Guadalquivir Estuary. *J. Fish Biol.* 61(suppl. A): 21-32.

Barbaro A., Francescon A., Bertotto D., Bozzato G., Di Maria I., Patarnello P., Furlan F., Colombo L. 2002. More effective induction of spawning with long-acting GnRH agonist in the shi drum, *Umbrina cirrosa* L. (Sciaenidae, Teleostei), a valuable candidate for Mediterranean mariculture. *J. Appl. Ichthyol.* 18: 192-199.

Basilone G., Guisande C., Patti B., Mazzola S., Cuttitta A., Bonanno

A., Vergara A.R., Maneiro I. 2006. Effect of habitat conditions on reproduction of the European anchovy (*Engraulis encrasicolus*) in the Strait of Sicily. *Fish. Oceanogr.* 15: 271-280.
Bell J.D., Rothlisberg P.C., Munro J.L., Loneragan N.R., Nash W.J., Ward R.D., Andrew N.L. 2005. Restocking and stock enhancement of marine invertebrate fisheries. *Adv. Mar. Biol.* 49: 1-370.
Bolger T., Connolly P.L. 1989. The selection of suitable indices for the measurement and analysis of fish condition. *J. Fish Biol.* 34: 171-182.
Born A.F., Immink A.J., Bartley D.M. 2004. Marine and coastal stocking: global status and information needs. In: Bartley D.M., Leber K.M. (eds), *Marine Ranching* Vol. 429. FAO Fisheries Technical Paper, pp. 1-12.
Butler G.L., Rowland S.J. 2009. Using underwater cameras to describe the reproductive behaviour of the endangered eastern freshwater cod *Maccullochella ikei. Ecol. Freshw. Fish* 18: 337-349.
Carrillo M., Zanuy S., Prat F., Cerdá J., Ramos E., Mañanós E., Bromage N. 1995. Sea bass (*Dicentrarchus labrax*). In: Bromage N., Roberts R.J. (eds), *Broodstock Management and Egg and Larval Quality*. Blackwell Science Publications, Oxford, UK, pp. 138-168.
Catalán I.A., Jiménez M.T., Alconchel J.I., Prieto L., Muñoz J.L. 2006. Spatial and temporal changes of coastal demersal assemblages in the Gulf of Cadiz (SW Spain) in relation to environmental conditions. *Deep-Sea Res. II* 53: 1402-1419.
Cerqueira R.V. 2002. Cultivo do robalo. In: Cerqueira R.V. (eds), *Cultivo do robalo: aspectos da reprodução, larvicultura e engorda*. Universidad Federal de Santa Catarina, Laboratorio de Piscicultura Marina, Florianópolis, Brazil, pp. 94.
Chao L.N. 1986. Sciaenidae. In: Whitehead P.J.P, Bauchot M.L., Hureau J.C., Tortonese E. (eds), *Fishes of the Eastern Atlantic and the Mediterranean*, Vol. II. UNESCO Pub., Paris, France, pp. 865-874.
Chatzifotis S., Panagiotidou M., Papaioannou N., Plavidis M., Nengas I., Mylonas C.C. 2010. Effect of dietary lipid levels on growth, feed utilization, body composition and serum metabolites (*Argyrosomus regius)* juveniles. *Aquaculture* 307: 65-70.
Chen Y., Jackson D.A., Harvey H.H. 1992. A comparison of von Bertalanffy and polynomial functions in modelling fish growth data. *Can. J. Fish. Aquat. Sci*. 49: 1228-1235.
Coleman F., Koenig C.C., Collins A. 1996. Reproductive style of shallow-water groupers (Pisces: Serranidae) in the eastern Gulf of Mexico and the consequences of fishing spawning aggregations. *Env. Biol. Fish.* 47: 129-141.
Craig S.R., Mackenzie D.S., Jones G., Gatlin D.M.III. 2000. Seasonal changes in the reproductive condition and body composition of free-ranging red drum, *Sciaenops ocellatus*. *Aquaculture* 190: 89-102.
Dadzie S. 2007. Vitellogenesis, oocyte maturation pattern, spawning rhythm and spawning frequency in *Otolithes ruber* (Schneider, 1801) (Sciaenidae) in the Kuwaiti waters of the Arabian Gulf. *Sci. Mar.* 71: 239-248.
Duncan N., Estévez A., Porta J., Carazo I., Norambuena F., Aguilera C., Gairin I., Bucci F., Valles R., Mylonas C.C. 2012. Reproductive development, GnRHa-induced spawning and egg quality of wild meagre (*Argyrosomus regius*) acclimatised to captivity. *Fish Phys. Biochem.* 38: 1273-1286.
Estévez A., Treviño L., Kotzamanis Y., Karacostas I., Tort L., Gisbert E. 2010. Effects of different levels of plant proteins on the ongrowing of meagre (*Argyrosomus regius*) juveniles at low temperatures. *Aquac. Nutr.* 17: 572-582.
Estrada M., Vives F., Alcaraz M. 1985. Life and productivity of the open sea. In: Margalef R. (eds), *Western Mediterranean*. Pergamon Press, Oxford, pp. 148-197.
FAO 2007. Food and Agriculture Organization, Fisheries Department, Fishery Information, Data and Statistics Unit. FISHSTAT Plus: Universal software for fisheries statistical time series. Version 2.32. 2000.
Fennessy S.T. 2000. Aspects of the biology of four species of Sciaenidae from the east coast of South Africa. *Est. Coast. Shelf. Sci.* 50: 259-269.
Fennessy S.T. 2006. Reproductive biology and growth of the yellowbelly rockcod *Epinephelus marginatus* (Serranidae) from South-East Africa. *Afr. J. Mar. Sci.* 28: 1-11.
Fernandez de Puelles M.L., Valencia J.M., Vicente L. 2004. Zooplankton variability and climatic anomalies from 1994 to 2001 in the Balearic Sea (Western Mediterranean). *ICES J. Mar. Sci.* 61: 492-500.
Fleming I.A., Gross M.R. 1993. Breeding success of hatchery and wild coho salmon (*Oncorhynchus Kisutch*) in competition. *Ecol. Applic.* 3: 230-245.
Fleming I.A., Jonsson B., Gross M.R., Lamberg A. 1996. An experimental study of the reproductive behaviour and success of farmed and wild Atlantic salmon (*Salmo salar*). *J. Appl. Ecol.* 33: 893-905.
Foucher R.P., Beamish R.J. 1980. Production of nonviable oocytes by pacific hake (*Merluccius productus*). *Can. J. Fish. Aquat. Sci.* 37: 41-48.
González-Quirós R., del Árbol J., García-Pacheco M.M., Silva-García A.J., Naranjo J.M., Morales-Nin B. 2011. Life history of the meagre *Argyrosomus regius* in the Gulf of Cádiz (SW Iberian Peninsula). *Fish. Res.* 109: 140-149.
Grau A., Crespo S., Riera F., Pou S., Sarasquete M.C. 1996. Oogenesis in the amberjack *Seriola dumerili* Risso, 1810. An histological, histochemical and ultrastructural study of oocyte development. *Sci. Mar.* 60: 391-406.
Grau A., Rodríguez-Rua A., Massutí-Pascual E., Jiménez M.T., Durán J., Jiménez-Cantizano R.M., Pastor E., Cárdenas S. 2007. Spawning of meagre *Argyrosomus regius* (Asso, 1801), using GnRHa. In: Aquaculture Europe 2007. European Aquaculture Society. pp. 439-440.
Grau A., Linde M., Grau A.M. 2009. Reproductive biology of the vulnerable species *Sciaena umbra* Linnaeus, 1758 (Pisces: Sciaenidae). *Sci. Mar.* 73: 67-81.
Griffiths M.H. 1996. Life history of the dusky kob *Argyrosomus japonicus* (Sciaenidae) off the east coast of South Africa. *S. Afr. J. Mar. Sci.* 17: 135-154.
Griffiths M.H., Hecht T. 1995. Age and growth of South African dusky kob *Argyrosomus japonicus* (Sciaenidae) based on otoliths. *S. Afr. J. Mar. Sci.* 16: 119-128.
Haddon M. 2001. *Modelling and Quantitative Methods in Fisheries.* Boca Ratón, Florida: Chapman and Hall/CRC, 424 pp.
Hamilton S.L., Caselle J.E., Standish J.D., Schroeder D.M., Love M.S., Rosales-Casian J., Sosa-Nishizaki O. 2007. Size-selective harvesting alters life histories of a temperate sex-changing fish. *Ecol. Applic.* 17: 2268-2280.
Hard J.J., Wertheimer A.C., Heard W.R., Martin R.M. 1985. Early male maturity in two stocks of Chinook salmon (Oncorhynchus tshawytscha) transplanted to an experimental hatchery in southeastern Alaska. *Aquaculture* 48: 351-359.
Houghton R.G., Last J.M., Bromley P.J. 1985. Fecundity and egg size of sole (*Solea sole* (L.)) spawning in captivity. *J. Cons. Int. Explor. Mer.* 42: 162-165.
Hunter J.R., Macewicz B.J., Lo N.Ch.H., Kimbrell C.A. 1992. Fecundity, spawning, and maturity of female Dover sole *Microstomus pacificus*, with an evaluation of assumptions and precision. *Fish. Bull. (United States)* 90: 101-128.
Hutchings K., Griffiths M.H., Field J.G. 2006. Regional variation in the life history of the canary drum *Umbrina canariensis* (Sciaenidae), in South African waters. *Fish. Res.* 77: 312-325.
Imsland A.K., Folkvord A., Grung G.L., Stefansson S.O., Taranger G.L. 1997. Sexual dimorphism in growth and maturation of turbot, *Scophthalmus maximus* (Rafinesque, 1810). *Aquac. Res.* 28: 101-114.
Jensen A.J. 1979. Energy content analysis from weight and liver index measurements of immature pollock (*Pollachius virens*). *J. Fish. Res. Board Can.* 36: 1207-1213.
Jiménez M.T., Pastor E., Grau A., Alconchel J.I., Sánchez R., Cárdenas S. 2005 Revisión del cultivo de esciénidos en el mundo, con especial atención a la corvina *Argyrosomus regius* (Asso, 1801). *Bol. Inst. Esp. Oceanog.* 21: 169-175.
Joaquim S., Matias D., Lopes B., Arnold W.S., Gaspar M.B. 2008. The reproductive cycle of white clam *Spisula solida* (L.) (Mollusca: Bivalvia): Implications for aquaculture and wild stock management. *Aquaculture* 281: 43-48.
Jonsson B. 1997. A review of ecological and behavioural interactions between cultured and wild Atlantic salmon. *ICES J. Mar. Sci.* 54: 1031-1039.
Jonsson B., Jonsson N. 2006. Cultured Atlantic salmon in nature: a review of their ecology and interaction with wild fish. *ICES J. Mar. Sci.* 63: 1162-1181.
Lagardére J.P., Mariant A. 2006. Spawning sounds in meagre *Argyrosomus regius* recorded in the Gironde estuary, France. *J. Fish*

Biol. 69: 1697-1708.
Lambert Y., Dutil J.D. 1997. Can simple condition indices be used to monitor and quantify seasonal changes in the energy reserves of Atlantic cod (*Gadus morhua*)? *Can. J. Fish. Aquat. Sci.* 54: 104-112.
Lim H.K., Le M.H., An C.M., Kim S.Y., Park M.S., Chang Y.J. 2010. Reproductive cycle of yellow croaker *Larimichthys polyactis* in southern waters off Korea. *Fish. Sci.* 76: 971-980.
Linde M., Palmer M., Alós J. 2011. Why protogynous hermaphrodite males are relatively larger than females? Testing growth hypotheses in Mediterranean rainbow wrasse *Coris julis* (Linnaeus, 1758). *Environ. Biol. Fish.* 92: 337-349.
Lloret J., Rätz H-J. 2000. Condition of cod (*Gadus morhua*) off Greenland during 1982-1998. *Fish. Res.* 48: 79-86.
Lowerre-Barbieri S.K., Chittenden M.E., Barbieri L.R. 1996. The multiple spawning pattern of weakfish in the Cheasepeak Bay and Middle Atlantic Bight. *J. Fish Biol.* 48: 1139-1163.
Lowerre-Barbieri S.K., Henderson N., Llopiz J., Walters S., Bickford J., Muller R. 2009. Defining a spawning population (spotted seatrout *Cynoscion nebulosus*) over temporal, spatial, and demographic scales. *Mar. Ecol. Prog. Ser.* 394: 231-245.
Luna L.G. 1968. *Manual of Histologic Staining Methods of the Armed Forces Institute of Pathology.* McGraw-Hill Book Company, New York.
Macchi G.J., Acha E.M., Militelli M.I. 2003. Seasonal egg production of whitemouth croacker (*Micropogonias furnieri*) in the Rio de la Plata estuary, Argentina-Uruguay. *Fish. Bull.* 101: 332-342.
Macpherson E., Raventos N. 2006. Relationship between pelagic larval duration and geographic distribution of Mediterranean littoral fishes. *Mar. Ecol. Prog. Ser.* 327: 257-265.
Maldonado-García M., Gracia-López V., Carrillo M., Henández-Herrera A., Rodríguez-Jaramillo C. 2005. Stages of gonad development during the reproductive cycle of the blackfin snook, *Centropomus medius* Günther. *Aquac. Res.* 36: 554-563.
Marino G., Azzurro E., Massari A., Finoia G., Mandich A. 2001. Reproduction in the dusky grouper from the southern Mediterranean. *J. Fish Biol.* 58: 909-927.
Marshall C.T., Kjesbu O.S., Yaragina N.A., Solemdal P., Ulltang Ø. 1998. Is spawner biomass a sensitive measure of the reproductive and recruitment potential of Northeast Arctic cod? *J. Fish. Aquat. Sci.* 55: 1766-1783.
Marshall C.T., O'Brien L., Tomkiewicz J., Köster F.W., Kraus G., Marteinsdottir G., Morgan M.J., Saborido-Rey F., Blanchard J.L., Secor D.H., Wright P.J., Mukhina N.V., Bjornsson H. 2003. Developing alternative indices of reproductive potential for use in fisheries management, case studies for stocks spawning, an information gradient. *J. Northw. Atl. Fish. Sci.* 33: 161-190.
Mayer I., Shackley S.E., Witthames P.R. 1990. Aspects of the reproductive biology of the bass, *Dicentrarchus labrax* L. II. Fecundity and pattern of oocyte development. *J. Fish Biol.* 36: 141-148.
Mayol J., Grau A.M., Riera F., Oliver J. 2000. Llista Vermella dels Peixos de les Balears. In: *Quaderns de Pesca, 4*. Govern de les Illes Balears, Grafiques Mallorca, Palma.
Merayo C.R. 1996. Seasonal changes in the biochemical composition of the muscle and liver of bib (*Trisopterus luscus* L.) (Pisces, Gadidae) from the Cantabrian Sea (N Spain). *Sci. Mar.* 60: 489-495.
Micale V., Maricchiolo G., Genovese L. 2002. The reproductive biology of blackspot sea bream *Pagellus bogaraveo* in captivity. I. Gonadal development, maturation and hermaphroditism. *J. Appl. Ichthyol.* 18: 172-176.
Monfort M.C. 2010. Present market situation and prospects of meagre (*Argyrosomus regius*), as an emerging species in Mediterranean aquaculture. In: FAO Studies and Reviews, Vol. 89. 28 pp.
Morales-Nin B., Grau A., Pérez-Mayol S., Gil M.M. 2010. Marking of otoliths, age validation and growth of *Argyrosomus regius* juveniles (Sciaenidae). *Fish. Res.* 106: 76-80.
Morales-Nin B., Geffen A.J., Pérez-Mayol S., Palmer M., González-Quirós R., Grau A. 2012. Seasonal and ontogenic migrations of meagre (*Argyrosomus regius*) determined by otolith geochemical signatures. *Fish. Res.* 127-128: 154-165.
Murua H., Saborido-Rey F. 2003. Female reproductive strategies of marine fish species of the North Atlantic. *J. Northw. Atl. Fish. Sci.* 33: 23-31.
Murua H., Lucio P., Santurtun M., Motos L. 2006. Seasonal variation in egg production and batch fecundity of European hake *Merluccius merluccius* (L.) in the Bay of Biscay. *J. Fish Biol.* 69: 1304-1316.
Mylonas C.C., Kyriakou Y., Sigelaki I., Georgiou G., Stephanou D., Divanach P. 2004. Reproductive biology of the shi drum (*Umbrina cirrosa*) in captivity and induction of spawning using GnRHa. *Isr. J. Aquacult.-Bamid.* 56: 75-92.
Nieland D.L., Wilson C.A. 1993. Reproductive biology and annual variation of reproductive variables of black drum in the northern Gulf of Mexico. *Trans. Am. Fish. Soc.* 122: 318-327.
Pears R.J., Choat J.H., Mapstone B.D., Begg G.A. 2006. Demography of a large grouper, *Epinephelus fuscoguttatus*, from Australia's Great Barrier Reef: implications for fishery management. *Mar. Ecol. Prog. Ser.* 307: 259-272.
Piner K.R., Jones C.M. 2004. Age, growth and the potential for growth overfishing of spot (*Leiostomus xanthurus*) from the Chesapeake Bay, eastern USA. *Mar. Freshwater Res.* 55: 553-560.
Piccolo G., Bovera F., De Riu N., Marono S., Salati F., Cappuccinelli R., Moniello G. 2008. Effect of two different protein/fat ratios of the diet on meagre (*Argyrosomus regius*) traits. *Ital. J. Anim. Sci.* 7: 363-371.
Prista N., Costa J.L., Costa M.J., Jones C.M. 2007. New methodology for studying large valuable fish in data poor situations: commercial mark-recapture of meagre *Argyrosomus regius* in the southern coast of Portugal. ICES CM 2007/O: 43.
Quéméner L. 2002. *Le maigre commun (Argyrosomus regius). Biologie, pêche, marché et potentiel aquacole*. Ifremer, Brest Cedex, 31 pp.
Quéro J.C. 1989. Sur la piste des maigres *Argyrosomus regius* (Pisces, Scianidae) du golfe de Gascogne et de Mauritanie. *Oceanis* 15: 161-170.
Quéro J.C., Vayne J.J. 1987. Le maigre, *Argyrosomus regius* (Asso,1801) (Pisces, Perciformes, sciaenidae) du golfe de Gascogne et des eaux plus septentrionales. *Rev. Trav. Inst. Pech. Marit.* 49: 35-66.
Ravaglia M.A., Maggese M.C. 2002. Oogenesis in the swamp eel *Synbranchus marmoratus* (Bloch, 1795) (Teleostei; synbranchidae). Ovarian anatomy, stages of oocyte development and micropyle structure. *Biocell* 26: 325-337.
Reñones O., Grau A., Mas X., Riera F., Saborido-Rey F. 2010. Reproductive pattern of an exploited dusky grouper *Epinephelus marginatus* (Lowe 1834) (Pisces: Serranidae) population in the western Mediterranean. *Sci. Mar.* 74: 523-537.
Roa R., Ernst B., Tapia F. 1999. Estimation of size at sexual maturity: an evaluation of analytical and resampling procedures. *Fish. Bull.* 97: 570-580.
Roo J., Hernandez-Cruz M.C., Borrero C., Schuchardt D., Fernández- Palacios H. 2010. Effect of larval density and feeding sequence on meagre (*Argyrosomus regius*; Asso, 1801) larval rearing. *Aquaculture* 302: 82-88.
Roumillat W.W., Brouwer M.C. 2004. Reproductive dynamics of female spotted sea trout (*Cynoscion nebulosus*) in South Carolina. *Fish. Bull.* 102: 473-487.
Sadovy Y., Shapiro D.Y. 1987. Criteria for the diagnosis of hermaphroditism in fishes. *Copeia* 1: 136-156.
Sadovy Y., Colin P.L. 1995. Sexual development and sexuality in the Nassau grouper. *J. Fish Biol.* 46: 961-976.
Sadovy Y., Cheung W.L. 2003. Near extinction of a highly fecund fish: the one that nearly got away. *Fish Fish.* 4: 86-99.
Shapiro D., Sadovy Y., McGehee M.A. 1993. Periodicity of sex change and reproduction in the red hind, *Epinephelus guttatus*, a protogynous grouper. *Bull. Mar. Sci.* 53: 1151-1162.
Sigelaki E., Papadaki M., Mitrizakis N., Mylonas C. 2011. Reproductive cycle of the meagre (*Argyrosomus regius*) in captivity. In: Aquaculture Europe 2011. European Aquaculture Society. pp. 396-397.
Silberschneider V., Gray C.A., Stewart J. 2009. Age, growth, maturity and the overfishing of the iconic sciaenid, *Argyrosomus japonicus*, in south-eastern, Australia. *Fish. Res.* 95: 220-229.
Stearns S.C., Crandall R.E. 1984. Plasticity for the age and size at sexual maturity: a life-history response to unavoidable stress. In: Potts G.W., Wootton R.J. (eds), *Fish Reproductive Strategies and Tactics*. Academic Press, New York, pp. 13-30.
Tixerant G. 1974. *Contribution à l'étude de la biologie du maigre ou courbine Argyrosomus regius (Asso) sur la côte mauritanienne.* Thèse d'université d'Aix-Marseille, 146 pp.

Tormosova I.D. 1983. Variation in the age at maturity of the North Sea haddock, *Melanogrammus aeglefinus* (Gadidae). *J. Ichthyol.* 23: 68-74.
Trippel E.A. 1995. Age at maturity as a stress indicator in fisheries. *BioScience* 45: 759-771.
Trippel E.A. 1999. Estimation of stock reproductive potential: History and challenges for Canadian Atlantic gadoid stock assessments. *J. Northw. Atl. Fish. Sci.* 25: 61-81.
Wilk S.J., Morse W.W., Stehlik L.L. 1990. Annual cycles of gonado-somatic indices as indicators of spawning activity for selected species of finfish collected from the New York Bight. *Fish. Bull.* 88: 775-786.
Wilson C.A., Nieland D.L. 1994. Reproductive biology of the red drum, *Sciaenops ocellatus*, from the neritic waters of the northern Gulf of Mexico. *Fish. Bull.* 92: 841-850.
Wootton R.J. 1990. *Ecology of Teleost Fishes*. Chapman and Hall, London, 404 pp.
Yamaguchi A., Todoroki T., Kume G. 2006. Reproductive cycle, sexual maturity and diel-reproductive periodicity of white croaker, *Pennahia argentata* (Sciaenidae), in Ariake Sound, Japan. *Fish. Res.* 82: 95-100.
Zohar Y. 1989. Fish reproduction: its physiology and artificial manipulation. In: Shilo M., Sarig S. (eds), *Fish Culture in Warm Water Systems: Problems and Trends.* CRC Press, Boca Raton, FL, pp. 65-119.
Zohar Y., Mylonas C. 2001. Endocrine manipulations of spawning in cultured fish: from hormones to genes. *Aquaculture* 197: 99-136.
Zohar Y., Abraham M., Gordin H. 1978. The gonadal cycle of the captivity-reared hermaphroditic teleost Sparus aurata (L) during the first two years of life. *Ann. Biol. Anim. Bioch. Biophys.* 18: 877-882.

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