Reproductive biology of the vulnerable species *Sciaena umbra* Linnaeus, 1758 (Pisces: Sciaenidae)

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SUMMARY: Reproductive biology of the brown meagre, *Sciaena umbra*, is described based on 171 specimens caught by trammel nets and spear gun from April 1998 to October 2000. Histological examination and gonadosomatic index suggest that the spawning season of the brown meagre in Balearic waters is from May to August and peaks in May and June. Seven stages of gonadal development were identified: immature, early developing, late developing, running, spent, recovering and resting. The frequency distribution of oocyte diameter reveals that brown meagre is an iteroparous, gonochoristic, seasonal multiple-spawning fish with aynchronous oocyte development. Size at first maturity was 25.4 cm of total length for males and 29.9 cm for females. Sex ratio varied with fish size, with a tendency for greater numbers of females in higher size classes. Weight-length relationships for both sexes, as well as for the total population, were significantly allometric positive. An analysis of the monthly variations of hepatosomatic index (HSI), and Le Cren's condition factor showed that HSI is not a good indicator of the lipid reserves of *S. umbra*. According to our results, current management measures for this species should be re-evaluated.

Keywords: *Sciaena umbra*, teleostean fishes, reproduction, spawning period, histology, Mediterranean Sea, Balearic Islands.

RESUMEN: BIOLOGÍA REPRODUCTIVA DE LA ESPECIE VULNERABLE *SCIAENA UMBRA* LINNAEUS, 1758 (PISCES: SCIAENIDAE). – Se ha estudiado la biología reproductiva de *Sciaena umbra* a partir de ejemplares capturados mediante trasmallo y arpón durante el periodo 1998-2000. El examen histológico y el índice gonadosomático sugieren que la época de puesta del corvallo en Baleares comprende los meses de mayo a agosto, presentando un pico de actividad reproductiva de mayo a junio. Se han identificado siete estadios de desarrollo gonadal: inmaduros, en desarrollo inicial, en desarrollo final, en puesta, agotamiento, recuperación y reposo. La frecuencia de distribución del diámetro del ovocito muestra que el corvallo es una especie iterópara, gonocórica, estacional, de múltiples puestas y desarrollo ovocitario asincrónico. La talla de primera madurez fue de 25.4 cm (longitud total) para los machos y de 29.9 cm para las hembras. La proporción de sexos varió en relación a la talla, con tendencia a favor de las hembras al aumentar la talla. La relación talla-peso de ambos sexos y de la población, fue alométrica positiva. El estudio de las variaciones mensuales en el índice hepatosomático (IHS) y el índice de condición de Le Cren indicó que el IHS no es un buen indicador de las reservas lipídicas de *S. umbra*. Según nuestros resultados, las medidas actualmente vigentes para esta especie deberían ser revisadas.

Palabras clave: *Sciaena umbra*, peces teleósteos, reproducción, periodo reproductivo, histología, mar Mediterráneo, Islas Baleares.

INTRODUCTION

The brown meagre, *Sciaena umbra,* is a littoral benthic Sciaenid that is distributed from the eastern Atlantic (from the English Channel to Senegal, included the Canary Islands) to the Mediterranean Basin, Black Sea and Sea of Azov. This species is not targeted by any particular fishery, but rather is a bycatch species whose commercial acceptance varies between locations (Bauchot, 1987). In the Medi-

terranean, the species is more abundant in southern and eastern regions, where it constitutes an important component of fisheries (eg. Algeria, Tunis, Egypt, Turkey), whereas it is rarely caught and not present in local fisheries statistics in some northern Mediterranean countries (Harmelin, 1991).

The brown meagre is currently considered a threatened Mediterranean species for which protection measures have been proposed (Chauvet, 1991; Harmelin, 1991; Mayol *et al.*, 2000). The northern Mediterranean stock has been considerably reduced and the North African stock is actually over-exploited due to artisanal, semi-industrial and recreational fishing (Bauchot, 1987). Moreover, it is a species which is highly vulnerable to spear fishing due to its indolent behaviour and accessibility, as has been repeatedly demonstrated in different NW Mediterranean marine reserves where this type of fishing has been prohibited (García-Rubies and Zabala, 1990; Francour, 1991; Harmelin *et al.*, 1995; Rius, 2007). In the Balearic Islands, the brown meagre is a valuable bycatch species for the artisanal fleet (trammel net, gill net and trap net) and a target species for recreational spear fishing. The latter extractive activity has a great impact around the islands (Riera *et al.*, 1998; Coll *et al.*, 2004), and its effect on both mean density and size is clearly evident in the 0 to 25 m depth range (Mayol *et al.*, 2000), which is easily accessed by spear fishers.

Despite its wide geographical distribution and its commercial and recreational value, few biological studies of the brown meagre have been conducted, and those available refer exclusively to the southern Mediterranean population (Chakroun and Ktari, 1981; Ning Chao, 1986; Bauchot, 1987; Chauvet, 1991; Harmelin, 1991; Harmelin and Marinopoulos, 1993, Chakroun-Marzouk and Katari, 2003).

Knowledge of the reproductive strategy and spawning pattern is essential for a comprehensive understanding of the population dynamics of any fish species (Hilborn and Walters, 1992; Hunter *et al.*, 1992) and to propose fishery management measures aimed at achieving sustainable exploitation of a vulnerable species (Mayol *et al.*, 2000), as is the case of the brown meagre is in the Balearic Islands. The reproductive behaviour of the brown meagre is cited in general ichthyological catalogues (Massutí, 1983; Ning Chao, 1986; Bauchot, 1987; Riera *et al.*, 1998). However, only two articles describe its spawning period, sexual cycle and age and size at first maturity. These are based on macroscopic observations

of gonad maturity and evolution of gonadosomatic index from brown meagres captured in Tunis (Chauvet, 1991; Chakroun-Marzouk and Katari, 2003). Maturity estimations are currently based on visual inspection, gonad weight or gonadosomatic index and hence little information is available on the histological gonadal development (Matsuyama *et al.*, 1987; Grau, 1992). Accuracy of macroscopic staging has been questioned (Hilge, 1977; Matsuyama *et al.*, 1987; West, 1990; Grau, 1992) and assessment of first maturity is only acceptable using histological criteria (Matsuyama *et al.*, 1987; West, 1990). Gonadosomatic index (GSI) provides a useful general indication of seasonal trends (Wilk *et al.*, 1990), but it is not a good predictor of gonad developmental stage and is not independent of fish size (de Vlaming *et al.*, 1982; West, 1990). The best means of assessing gonadal activity is to examine gonad histology (de Vlaming *et al.*, 1982) and, depending upon the nature of the study, it may be the only satisfactory method (West, 1990).

The main objectives of this study were therefore: 1) to carry out, for the first time, a histological classification of the maturity stages of *S. umbra* gonads in order to investigate its spawning activity and spawning pattern based upon seasonal variation in the prevalence of the different gonad developmental stages; 2) to establish size at maturity on the basis of these criteria in order to clarify the reproductive structure of brown meagre populations in the Balearic Islands; 3) to provide an in-depth analysis of the annual cycle of *S. umbra* by studying different indices related to its reproduction; and 4) to describe and identify the reproductive strategy of brown meagre in waters of the Balearic Islands.

MATERIALS AND METHODS

Sampling

A total of 171 specimens of *S. umbra* (25.2 - 53.1 cm total length) captured from Balearic coastal wild stock were examined in this study (Fig. 1). Of these, 51 were captured by experimental trammel net fishing conducted between May and September, while the remaining 120 were caught during spear fishing competitions which took place between April and October. All specimens were obtained from 1998 to 2000.

Whole fish were measured (± 0.1 cm total length), weighed (± 0.1 g), sexed and dissected. Sex ratio was
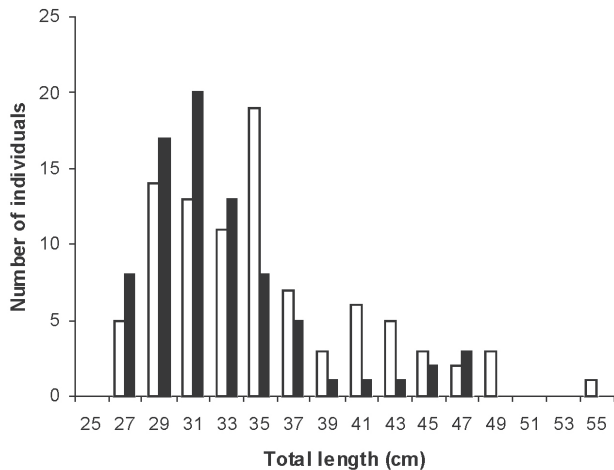
FIG. 1. – Length-frequency distribution of fished *Sciaena umbra* analysed in the present study (solid bars: male; clear bars: female).

calculated according to selected fish size classes. Gonads and liver were removed, weighed (± 0.01 g) and preserved in 10% buffered formalin. A segment of the central part of either of the two gonadal lobes and the liver were taken for histological analysis. These segments were embedded in paraplast (livers, testes and undeveloped ovaries) or hydroxyethyl methacrylate (ripening and ripe ovaries), and sectioned at a thickness of 3-4 µm (paraplast method) or 1-2 µm (methacrylate method). Sections were stained with Toluidine Blue and with Mayer's haematoxylin and eosin (H/E; Luna, 1968) for general histology.

Histological examination

The series of morphological changes occurring during oocyte development follow a similar pattern in most species of oviparous fish. Thus, we used a modification of the terminology used in the histological description of oocyte development employed by Grau *et al.* (1996). In order to accurately assess the pattern of oocyte development, oocyte frequency-distributions were also determined from histological sections. The value of determining oocyte size-frequency distributions lies in being able to associate developmental characteristics with any given size class (West, 1990). Oocyte measurements were performed on running ovaries at the spawning period to observe the formation of a well developed hiatus between the standing stock of unyolked oocytes and the yolked oocyte stock, only detected at this stage in brown meagre ovaries. In order to obtain a true representative oocyte count with the minimum bias towards a particular oocyte size, counts were made of

all oocytes present in 5 microscopic fields using a 4x objective. Oocyte size, obtained by taking the mean and maximum diameter, was only recorded from those oocytes which had been sectioned through the nucleus (Foucher and Beamish, 1980). Measurements included more than 700 oocytes per gonad. The increase in size of the nucleus with growth is relatively small, and the bias towards larger cells is minimised (Foucher and Beamish, 1980), so a correction factor was not applied to the observed oocyte size frequency measured in histological sections because the purpose of our analysis was only to compare oocyte size frequency distributions between individuals and not to quantify oocyte abundances. Liver sections were examined to determine the presence or absence of vacuoles in the hepatocytes, with liver vacuolisation being considered an indicator of the presence of lipid depots in this organ, as has also been found in previous studies (Rueda-Jasso *et al.*, 2004).

Data analysis

The proportion of mature specimens in relation to TL and sex was determined for 55 females and 64 males by fitting the data to a logistic model. The model was:

$$p = (e^{a+b \cdot TL + b_2 \cdot SEX + b_3})(1 + e^{a + b1 \cdot TL + b_2 \cdot SEX + b_3})^{-1}$$

where p is the probability of being mature, a and b_n are constants and regression slopes respectively, and TL (total length) and SEX are the independent variables. The model was then used to calculate the size at which 50% of fishes were mature (L50), which habitually represents the minimum size at sexual maturation in fisheries management. In the analysis, immature fishes were those with gonads at stage I, while mature fishes were made up of grouped individuals with gonads at stages III, IV and V.

The relationship (WLR) between weight (W) and total length (TL), $W = aTL^b$ was converted into its logarithmic expression: $\ln a + b \ln TL$. The parameters *a* and *b* were calculated by least-square regression, as was the coefficient of determination (r^2). The *b* value of the species was tested by a *t*-test ($\alpha = 0.05$) in order to verify whether it was significantly different from 3.

Three reproductive indices were employed. These were gonadosomatic index (GSI), hepatosomatic index (HSI) and Le Cren's (1951) relative condition

factor, which are defined as follows:

$$GSI = (GW/BW) \times 100$$
$$HSI = (LW\ BW) \times 100$$
$$K = (BW/aTL^b) \times 100$$

where BW = total ungutted body weight (g), GW = gonad weight (g), LW = liver weight (g) and TL= total length (cm). The parameters *a* and *b* were calculated by least-squares regression. As brown meagre exhibit an allometric growth different from 3 in the study area (Morey *et al.*, 2003; present study), Le Cren's index should be chosen to measure the body condition instead of Fulton's index (Bolger and Connolly, 1989).

Variations in the mean of these indices during the reproductive period were tested using one-way analysis of variance. The post-hoc Tukey's test was performed to determine pair-wise differences.

HSI is often used as an indicator of condition and nutritional status of fish (Rueda-Jasso *et al.*, 2004). Demersal fishes such as brown meagre tend to store lipid primarily in their livers (Sheridan, 1988; Sargent, 1997; Craig *et al.*, 2000). In this species the hepatosomatic index can therefore be considered an indirect index of the lipid energy status (Craig *et al.*,

2000). To investigate the accuracy of the hepatosomatic index (HSI) as an estimate of energy status, a two-way ANOVA was calculated to test the effects of liver vacuolisation and SEX on HSI (liver relative weight). The values of HSI were log transformed to normalise the data distribution.

RESULTS

Maturity staging of the gonads

The general histology of the ovaries of brown meagre, *S. umbra,* reveals that it is a gonochoristic, seasonal multiple-spawner fish. We could distinguish the presence of postovulatory follicles, together with a heterogeneous population of secondary developing oocytes in histological sections of the ovaries of reproductively active females. A large population of oocytes remained at the primary growth phase. These observations indicate that brown meagre is a serial batch spawner. Therefore, the microscopic maturity stages can be appropriately represented by the most advanced oocyte development stage present in the ovary within histological observations (West, 1990).

TABLE 1. – Histological characteristics of the maturity stages of the gonads of *Sciaena umbra*

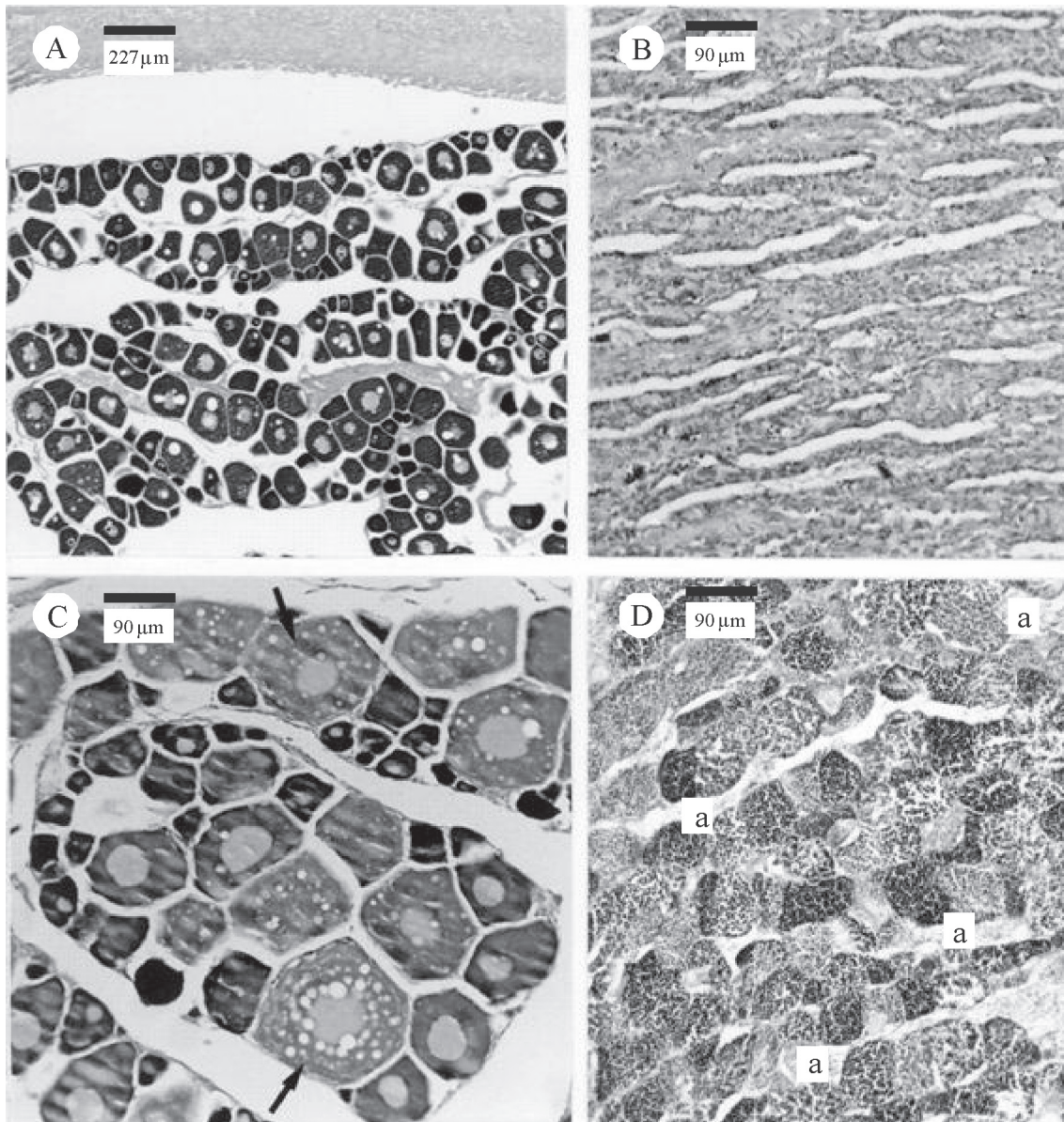| MATURITY STAGE	OVARY	TESTES
I. Immature	Wide ovarian cavity. Lamellae containing oogonia and primary oocytes.	Spermatogenesis has started but testes lack a well-defined tubular system.
Developing immature (or developing virgin)	Smaller ovarian cavity. Lamellae containing oogonia, primary oocytes and oocytes at lipid globule stage (LGS) during spawning period.	Tubules are well developed. Spermatogenesis is active and spermatozoa can be observed during reproductive season in some tubules (10-40%).
II. Early developing	Lamellae fill ovarian cavity. Very few oogonia; primary oocytes numerous. Oocytes at LGS and at CAS (cortical alveoli stage) can be observed	Spermatogenesis activity is generalised in testes. Spermatogonia are abundant. Spermatozoa can be observed in some tubules.
III. Late developing	Oocyte at all stages of development. Very few oogonia. Postovulatory follicles not seen.	Spermatogenic tubules are well formed and stroma between them is very limited. Spermatogenic cysts at all stages of development are present. Spermatozoa can be observed in the majority of tubules, but not in all.
IV. Running	Oocyte at all stages of development. Numerous postovulatory follicles. Ovarian cavity increases in size as spawning proceeds.	Spermatogenic activity is intense. Greatly enlarged tubules and vas deferens are fully filled with spermatozoa.
V. Spent	Wide ovarian cavity. Lamellae with numerous atretic vitellogenic oocytes and postovulatory follicles.	Tubules and vas deferens are full of spermatozoa, but spermatogenic activity is very limited.
VI. Recovering	Wide ovarian cavity. Primary oocytes and oogonia numerous. Corpus albicans (belonging to postovulatory follicles or atretic oocytes) are present. No vitellogenic oocyte.	Wall of spermatogenic tubules is full of spermatogonia. Residual spermatozoa are present at the lumen of spermatogenic tubules and vas deferens.
VII. Resting	Ovaries with a thick ovarian wall. Primary oocytes, oogonia and oocytes at LGS present.	Tubules are small in volume and stroma between them is well developed. They are full of spermatogonia, and some spermatogenic residual activity can be seen on their walls.

FIG. 2. – Photomicrographs of the gonads of the brown meagre at different stages of maturity. (A): Ovary at resting period. Only oogonia, primary oocytes and oocytes at LGS stage can be seen, (B): Testes at resting period. Notice the absence of spermatogenic activity, (C): Ovary at early developing period. Oocytes at cortical alveoli stage (arrow) are present, (D): Testes at early developing period. An intense spermatogenic activity is observed. (a) Spermatozoa.

The testes of brown meagre are of the lobular type (Nagahama, 1983), also called unrestricted spermatogonial testis-type (Grier, 1981), because spermatogonia are distributed along the entire length of the tubule and not only restricted to the distal terminus. Structural seasonal changes observed in the testes of brown meagre revealed that it is a seasonal spawner, with distinct stages of testes development throughout the annual reproductive cycle.

We described seven different developmental stages of brown meagre gonads based on histological examination (Table 1). We only examined develop-ing immature gonads during the breeding season, as during the resting period it is very difficult to distin-guish between developing immature gonads and the resting gonads of an adult. Stage I represents those fish which are not able to attain maturity. Gonads at Stage I include immature gonads and developing immature gonads. No yolked oocytes were present and spermatogenic tubules were not completely developed. Stage II represents early developing go-nads of an adult fish, prior to the spawning period (Fig. 2c, d). Gonads at stage III appeared to have sufficient chance to spawn. The presence of gonads
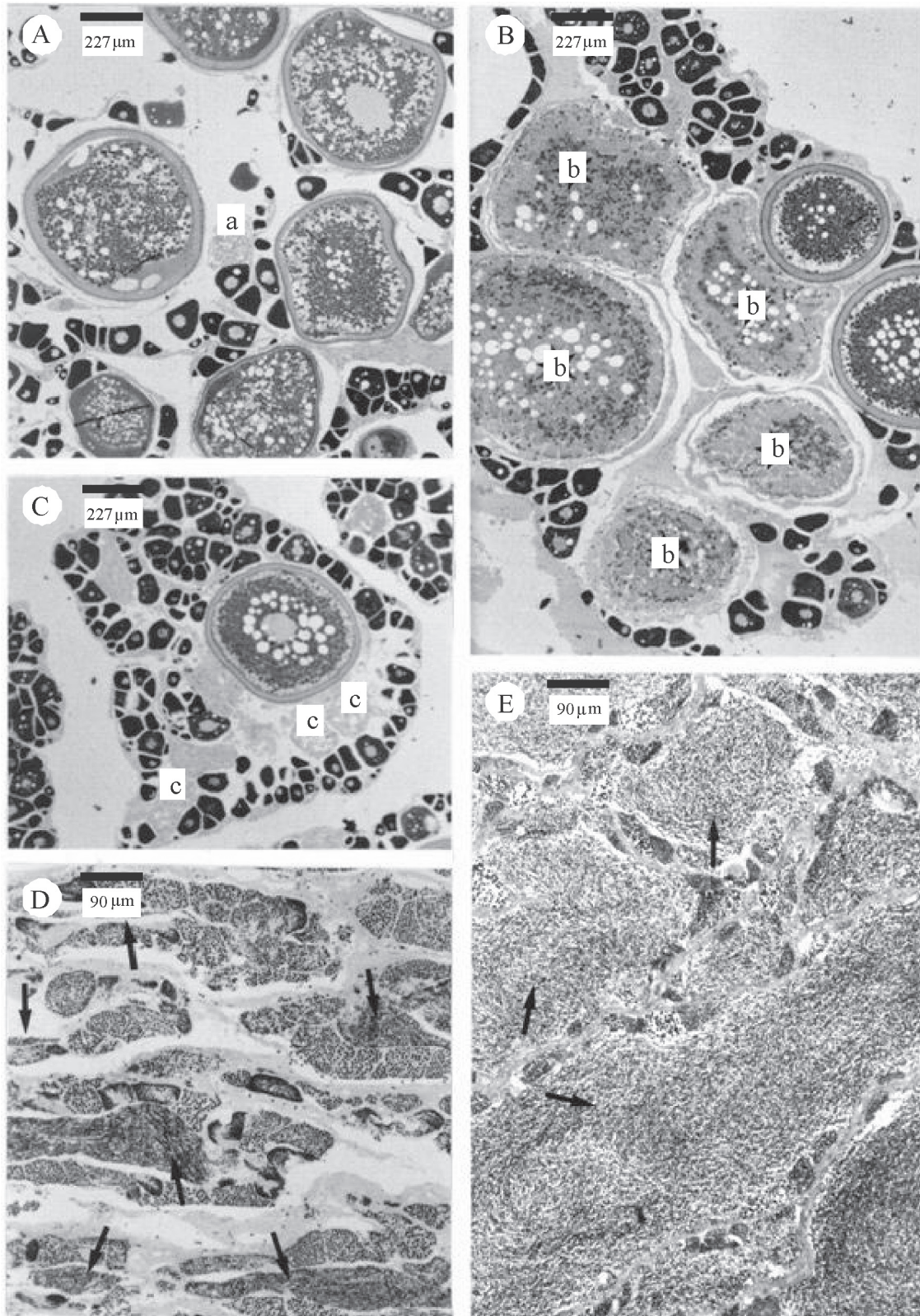
FIG. 3. – Photomicrographs of the gonads of *Sciaena umbra* at different stages of maturity. A: Running ovary of an adult spawner. Postovulatory follicles (a) can be seen. B: Spent ovary with numerous atretic vitellogenic oocytes (b). C: A young running female at spawning period. Notice the abundance of primary oocytes and LGS oocytes with some vitellogenic oocytes. Postovulatory follicles (c). D: Running testes at the beginning of the spawning period. Spermatogenic activity is intense and tubules are filled with spermatozoa (arrow). E: Spent testes. Tubules are fully filled of spermatozoa (arrow), but spermatogenic activity is very limited.

at stage IV (Fig 3a, c, d) indicates the beginning of the spawning period (Fig. 3b, e). In ovaries at stage IV, we distinguished the presence of postovulatory follicles together with a heterogeneous population of secondary developing oocytes; this indicates that brown meagre spawns more than once a season. The beginning of the post-spawning period is indicated by the presence of gonads at stage V (spent gonads). In the post-spawning period, some recovering gonads (stage VI) could be observed. This stage is characterised by the increase in number of gonia in both sexes. The presence of gonads at stage VII (resting; Fig. 2a, b) indicates the beginning of the resting period.

Oocyte size-frequency distributions

Figure 4 shows the oocyte size-frequency histograms determined from histological sections for 3 running adult brown meagre ovaries. Late-developing ovaries showed the same oocyte distribution as in Figure 4a and were therefore not included in the figures. Oocytes in all stages of development were present. There were oocytes undergoing vitellogenesis (200-600 µm), oocytes at the cortical-alveoli stage (140-190 µm) and primary oocytes (< 120 µm). These histograms show a continuous oocyte size-frequency distribution pattern in some running ovaries (Fig. 4a,b), but two size groups of oocytes with a clear hiatus (180 µm in size) between previtellogenic and vitellogenic oocytes can be distinguished in ovaries from mid-spawning fish (Fig. 4c). All these features indicate that the brown meagre exhibits an asynchronous ovarian development organisation, because the asynchrony in oocyte development is found in pre-spawning and running ovaries. However, this asynchrony doesn't persist as spawning progresses and a clear hiatus develops during spawning. The different modes in the continuous oocyte size-frequency distribution indicate the presence of several batches.

Reproductive cycle of brown meagre

The month-frequency distribution of the maturity stages of adult specimens of brown meagre is shown in Figure 5. Not all breeders are at the same gonadal developmental stage in a month. Running females were found from May to August while running males were found from May to September. A spawning activity peak occurs in May-June, when
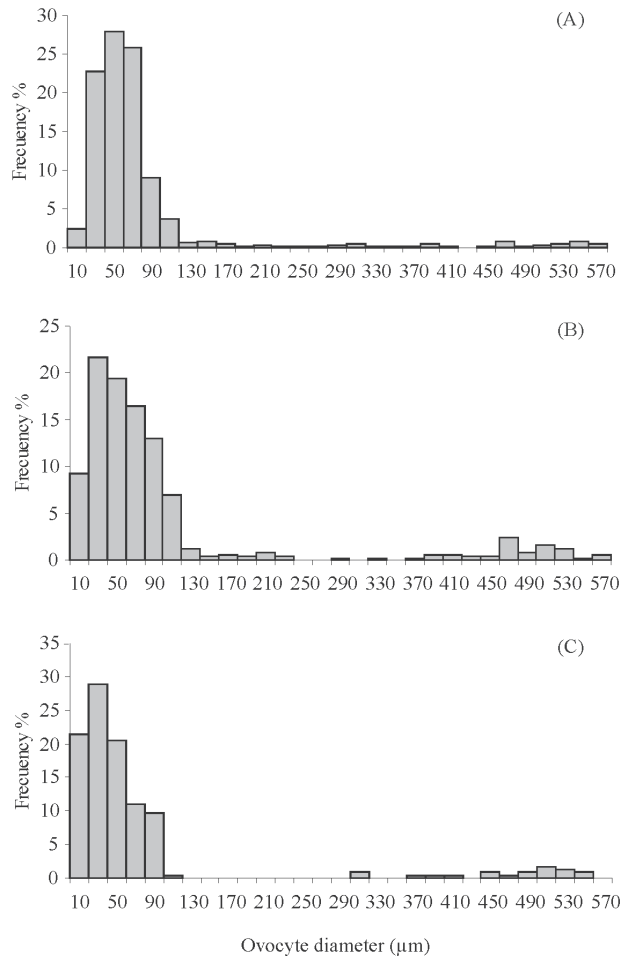

FIG. 4. – Size-frequency distribution of oocytes determined from histological sections for 3 spawning brown meagre females. A, 25 July 1998; B, 26 July 1998; C, 26 July 1998 (oocyte diameter in µm).
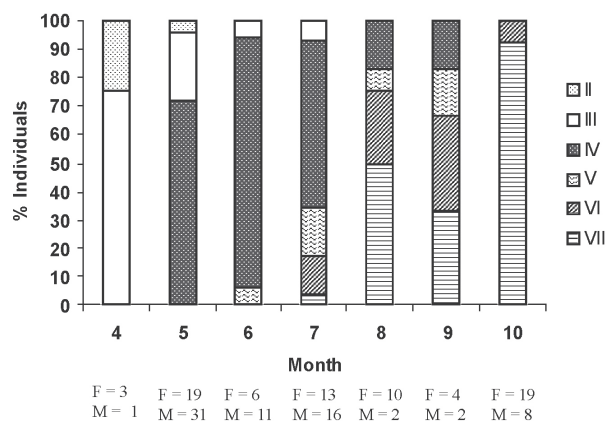

FIG. 5. – Monthly distribution of *Sciaena umbra* adult specimens at each gonadal stage during the sampling period (F, female; M, male).

more than 70% of gonads are running gonads. Some post-spawning and resting gonads can already be observed during June and July, respectively. Thus,
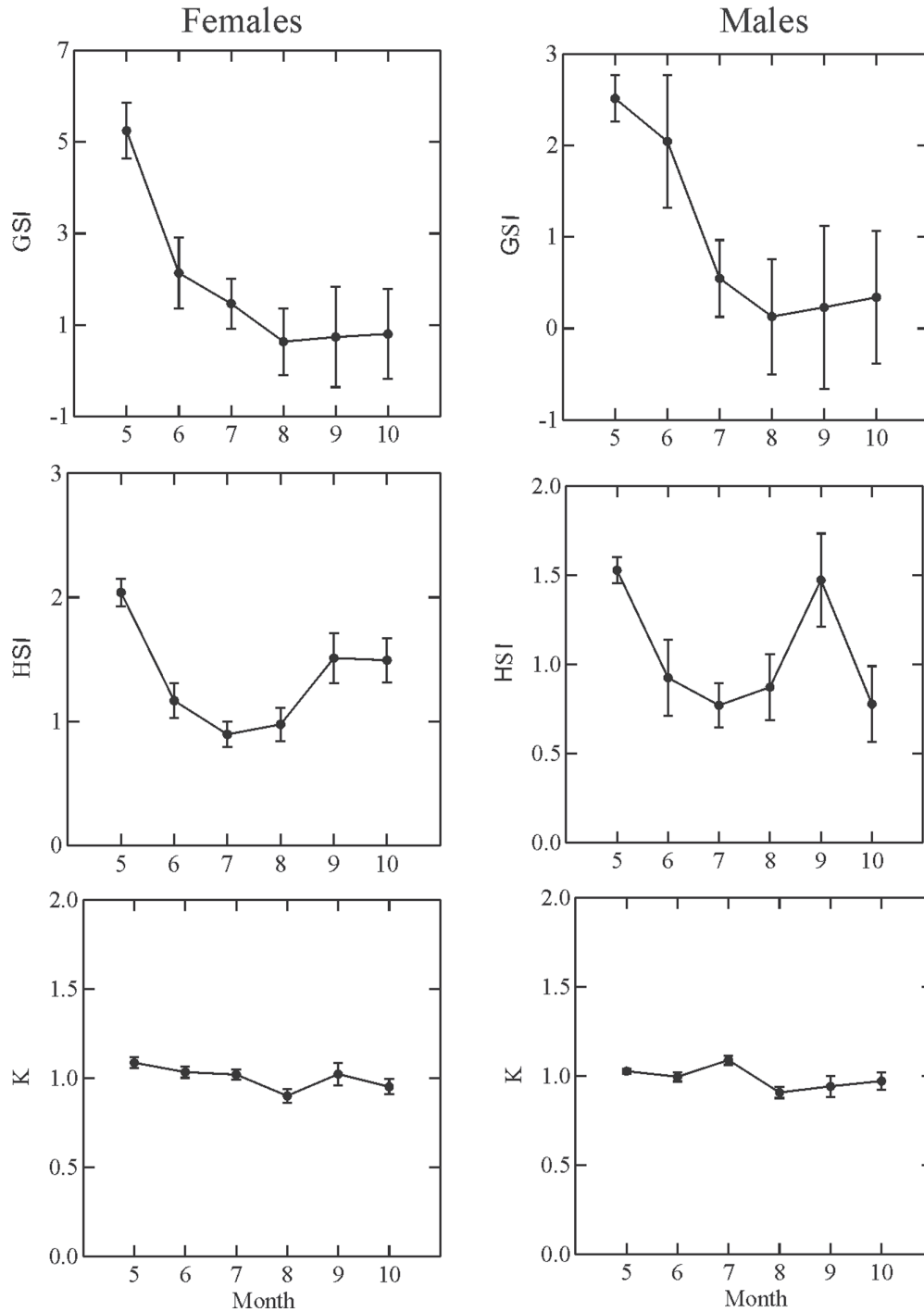
FIG. 6. – Trends of gonadosomatic index (GSI), hepatosomatic index (HIS) and condition factor (K) for both sexes.

the spawning season of brown meagre in the Balearic Islands extends from May to August, with the post-spawning period beginning in June and the resting period in July. The beginning of the developing period was not detected in the present study as the sampling method was based on samples taken outside the winter period in which we would expect to see these stages.

Trends in GSI, HSI and K

GSI values were higher in the months from May to July, with the peak value being reached in May, followed by a progressive decrease in the index during July. The index values for May were significantly higher for males (F = 6.116; df (5, 40); $P<0.001$) and females (F = 7.086; df (5, 49); $P<0.001$) (Fig. 6).

This period coincides with that of the higher proportion of spawner specimens (in stage IV). In August, the index fell to less than 1% and the proportion of running individuals was low (16.7%), with the majority being at post-spawning stages. The GSI index remained below 1% during September and October. The proportion of somatic weight devoted to gonads was lower for males in all months.

HSI values varied significantly (males: F = 8.289; df (5, 40); *P*<0.01; females: F = 13.881; df (5, 49); *P*<0.001) (Fig. 5). It is notable that, for both sexes, the highest values appeared in May and September and values remained lower from June to August.

In both sexes, the annual development of *K* was not very marked, with only a slight drop in August (Fig. 6). However, there were significant differences between August and May for females (F = 3.295; df (5, 71); *P*<0.025), and between August and May and July for males (F = 4.606; df (5, 56); *P*<0.01).

Gonad weight and GSI of mature fish

The relationships between gonad weight and GSI of brown meagre mature specimens (stage IV) and fish size are shown in Figure 7. There were significant linear relationships between gonad weight and body length for both sexes (Fig. 7a). The equation for females was:

$$lnGW = -19.094 + 6.133 \, lnTL$$
$$(n = 19; r^2 = 0.56; P<0.001)$$

and for males was:

$$lnGW = -30.526 + 9.420 \, lnTL$$
$$(n = 27; r^2 = 0.40; P<0.001)$$

The GSI was poorly correlated with fish size for both sexes (Fig. 7b). Large fish had relatively larger gonads compared with body weight, although the data were more dispersed and showed a poor linear fit (Fig. 7b). The correlation index was 0.219 (n = 19; *P*<0.05) for females, and 0.301 (n = 27, *P*<0.01) for males.

Population composition

The methods used for sampling brown meagre during this study are biased towards the capture of adult specimens, and this is clearly shown in the length frequency distribution, which lacked indi-
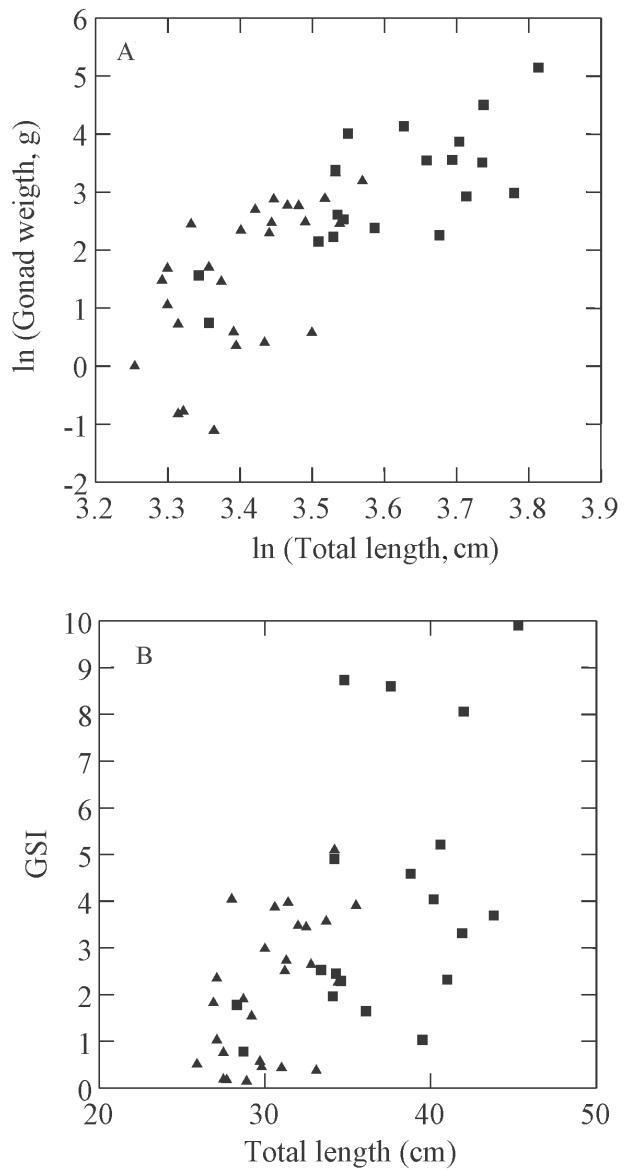

FIG. 7. – A, relationship of total length and gonadal weight at stage IV for males (square) and females (triangle). B, relationship of total length and gonadosomatic index (GSI) at stage IV for males (square) and females (triangle).

viduals below 25 cm TL (Fig. 1). Overall, females outnumbered males, particularly in the larger size classes. In fact, the proportion of males and females varied with fish size. A sex ratio of 1:0.76 skewed toward the males was observed for fishes below 31 cm TL. In contrast, the sex ratio of 1:1.32 favoured females in the specimens that ranged between 31 and 40 cm TL. Above 40 cm TL the sex ratio in favour of females was even more extreme at 1:2.57. The total sex ratio of the sampled population was 1:1.6

Weight-length relationships for both sexes, as well as for the total population, were significantly al-

TABLE 2. – Length-weight linear relationship of *Sciaena umbra*. (*): Slope of ln-transformed data significantly different from 3 using a *t*-test (*p*<0.05)

L-W	a	b	r^2	n	*t*-test
Population	0.0041	3.322	0.96	160	6.313*
Males	0.0029	3.425	0.97	63	5.326*
Females	0.0046	3.298	0.95	78	3.625*
Mature males	0.0031	3.410	0.96	31	3.347*
Mature females	0.0033	3.387	0.94	21	2.058

lometric positive. During the spawning period, adult running females and males also showed an allometric positive weight-length relationships, but in this case only the slope of the male regression differed significantly from 3 (Table 2).

Maturity sizes

The effect of the interaction between TL and SEX did not significantly affect the maturation probability curve (*P* = 0.266) (Fig. 8). We therefore removed the interaction from the model. The effects of TL and SEX on L50 were highly significant (TL: *z* = 4.239,<0.001; SEX: *z* = 3.689,<0.001). Size at first maturity differed between sexes, with males reaching maturity at a smaller size than females. The estimated value of L50 was 25.4 cm for males and 29.9 cm for females.

HSI and energy status

There were no differences in the HSI for the females between the reproductive and non-reproductive periods (n = 25 and 29; *t* = 1.604; *P* = 0.116), or between sexes during the same periods (for the reproductive period: n females = 25 and n males = 34; *t* = 0.636; *P* = 0.528; for the non-reproductive period: n females = 19 and n males = 7; *t* = 1.002; *P* = 0.326). However, in the case of males there was a difference in the HSI between the two periods (*t* = 2.208; *P*<0.05).

Two-way ANOVA did not reveal any significant effects of SEX or vacuolisation in the mean HSI of fishes (*P* = 0.1215, *P* = 0.7565, respectively; n = 135). There was a significant interaction between SEX and vacuolisation (*P* = 0.045). The lack of a difference between the relative mean weight of vacuolised livers and that of non-vacuolised livers was not expected, nor was the lack of a difference between sexes for the mean relative weight of vacuolised livers.
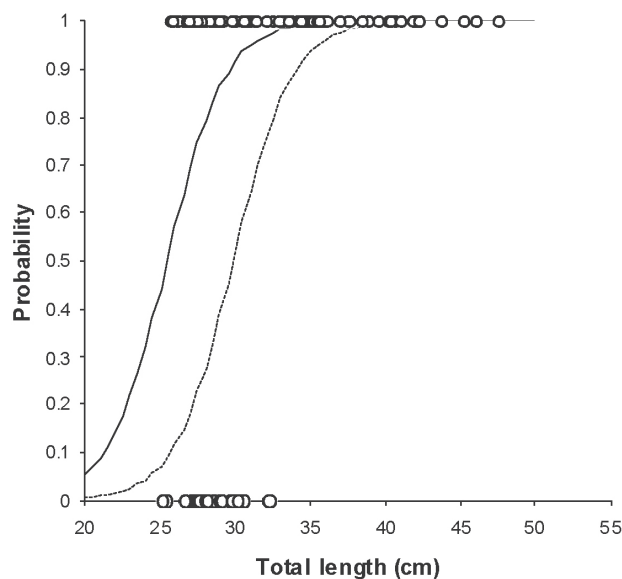

FIG. 8. – Probability curve of maturation of *Sciaena umbra* for males (solid line) and females (dashed line). Immature category grouped fishes at stage I, and mature fishes at stages III, IV and V.

Vacuolised livers show round, small to medium-sized droplets interspersed in the cytoplasm of parenchymal hepatic cells. The nucleus is generally located in a central position.

DISCUSSION

Reproductive pattern

To appropriately estimate the fecundity and reproductive potential of a species one must previously identify the mode in which mature eggs are developed and spawned (Murua *et al.*, 2003). Fecundity is easily measured in determinate spawners (Horwood and Greer Walker, 1990) and total fecundity calculated in pre-spawning individuals undergoing late vitellogenesis is considered to be equivalent to the potential annual fecundity (Murua *et al.*, 2003. In our study oocyte size frequency distributions indicated that the brown meagre exhibits an asynchronous oocyte development pattern. This means that oocytes at all stages of development can be distinguished at any one time, which is the definition of an asynchronous ovary (Wallace and Selman, 1981). However, a break in the size frequency distribution, of about 180 μm in size, was clearly observed as spawning proceeded. 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). Such an asynchronous ovarian configuration is typical of iteroparous species, which in temperate waters are typically small pelagic species with very protracted spawning seasons, in which yolk accumulation relies mostly on the food available in the environment at that moment (Murua and Saborido-Rey, 2003). Brown meagre is, however, a typical temperate large demersal species with a relatively protracted spawning season, and therefore does not meet this general assumption. Moreover, in asynchronous indeterminate species egg release is concurrent with oocyte recruitment, and hence ovary weight changes only slightly throughout most of the spawning season, showing either a dome-shape GSI curve or simply no trend at all (Alonso-Fernández *et al.*, 2008). Thus, the presence of a peak in brown meagre GSI, and the sharp decrease in this index, indicate a quick egg loss without replacement, which fits well with determinate fecundity. Moreover, the presence of a break in the oocyte size-frequency distributions during spawning, separating the yolked oocyte stock from the reservoir of unyolked oocytes, clearly indicates that the production of new oocytes to be spawned has ceased and that the annual fecundity is determinate (Murua and Saborido-Rey, 2003). However, despite this evidence supporting a determinate fecundity strategy in brown meagre, we believe that other determination criteria should be considered when the species in question has a hiatus which develops during spawning, as is the case with the brown meagre. Further assessment of fecundity would increase our knowledge of the state of the brown meagre stock in the Balearic Islands and will benefit basic fisheries research for the species.

On the other hand, the population of oocytes undergoing secondary growth is asynchronous, because they are not all at the same stage of development. This implies that the brown meagre is a "batch or fractional spawner", i.e. eggs are released in batches over a relatively protracted period (Mayer *et al.*, 1990; Murua and Saborido-Rey, 2003). Most of the commercially important cold and temperate water fishes are batch spawners (Murua and Saborido-Rey, 2003) and all the Sciaenidae studied are group-synchronous or asynchronous batch spawners (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). Gonads were classified in seven developmental stages based on histological analysis. In running females postovulatory follicles coexisted with yolk stage oocytes, again indicating that the brown meagre is a batch multiple spawner, spawning more than once in a single spawning season. Moreover, the presence of spent ovaries is further evidence that the brown meagre is a determinate spawner (West, 1990). Our histological data reveal that brown meagre exhibit a spawning season that could be considered as slightly protracted because it extends over 4 months (from May to August). Running male specimens continue into September, which can be expected as it is common for male fish to have a longer spawning period than females in Balearic waters (pers. obs.). A lack of population synchrony in gonadal development can also be observed, with not all the breeders showing the same ovarian maturity stage in a month. This extended breeding season appears to be typical of sciaenids in subtropical waters (Druzhinin, 1974), and as does spawning in spring and summer (Wilson and Nieland, 1994; Lowerre-Barbieri *et al.*, 1996; Francescon and Barbaro, 1999; Fennesy, 2000; Macchi *et al.*, 2003; Roumillat and Brouwer, 2004; Hutchings *et al.*, 2006; Yamaguchi *et al.*, 2006). Results from our histological data contrast with those from Tunisian waters that suggested a shorter spawning period, i.e. from July to August (Chauvet, 1991; Chakroun-Marzouk and Ktari, 2003). This difference could be due to differences in accuracy of staging methods rather than in spawning periods between localities: macroscopic staging is prone to errors (West, 1990) and the onset of spawning can only be detected microscopically (West, 1990; Grau, 1992). It is therefore likely that the brown meagre in Tunisian waters has a more protracted spawning period than was previously reported.

Trends of biological indices

The higher values of GSI in May and June for the Balearic brown meagre fit well with a spring-summer spawning. Other investigators (Chakroun-Marzouk and Ktari, 2003) have used the GSI to delineate the spawning season in brown meagre. Though the GSI provided a good approximation of the spawning season, histological data alone provided more accurate evidence. In temperate seas such as the Mediterranean there are distinct annual cycles of light intensity, temperature, nutrients and winds which drive produc-

tivity cycles. The timing and duration of spawning in fishes is generally accepted to coincide with periods in which environmental conditions are favourable for larval survival and growth, which are also periods in which spawning adult condition is optimal and their chance of survival is also high (Sadovy, 1996). In our case the spawning season started in May, which is the time when water temperature is rising in the Balearic Islands (Fernandez de Puelles *et al.*, 2004). Spawning and the subsequent planktonic life of most littoral species in the Mediterranean also take place in spring and summer, when water temperature and phyto- and zooplankton productivity is highest (Estrada *et al.*, 1985; Macpherson and Raventos, 2006). Moreover, Mediterranean infralittoral vegetal communities (algae and seagrass) begin to grow at this time, showing the most developed coverage and exuberance at the beginning of July (Ballesteros, 1991; Alcoverro *et al.*, 1997), when brown meagre juveniles settle in the Balearic Islands (J. Coll, pers. comm.). This temporal coincidence permits newly-settled brown meagre juveniles to find more feeding resources and protection inside seagrass meadows and infralittoral algae, therefore sustaining their rapid growth and development at a time of optimal nutrient availability and high water temperatures. Wild temperate fish undergo seasonal changes in growth and energy storage (Craig *et al.*, 2000), depleting protein and lipid reserves during gonadal growth (Brett and Groves, 1979). In general, HSI is inversely associated with GSI (Maddock and Burton, 1999; Craig *et al.*, 2000). This tendency is not clear in brown meagre, with the two indexes showing approximately a parallel decline from May to August, and a posterior divergence from September to October, when the HSI increases faster than the GSI. On the other hand, Condition Factor (K) remains practically constant throughout the sample period, with only a slight drop in the index in August, coinciding with the cessation of spawning. This indicates that the condition of the brown meagre is little influenced by reproductive effort, as revealed by the high positive WLR observed during the spawning season, which is in contrast with previous reports (Chakroun-Marzouk and Ktari, 2003). On the other hand, fish species which undergo hypophagia during their spawning season experience drastic variations in protein or lipid content of muscle (Nelson and McPherson, 1987; Meefe, 1993). The brown meagre spawning season coincides with the time of maximal water temperatures at the Balearic Islands (Fernandez de Puelles *et al.*, 2004), and the maintenance of condition during these months could reflect active feeding of the species during the period of maximum somatic growth.

In general, ovary size in fishes increases with stage of development and with fish size and/or weight (Buñag, 1956). For example, Matsuyama *et al.* (1987) and Matsuura *et al.* (1987) observed that there is an increase in the gonad weight and GSI with age/length in the porgy, *Pagrus major,* with mature reproductive organs. In the case of the brown meagre, we found that in the case of mature specimens with gonads at stage IV, the gonad weight tended to increase with fish size, but its relative weight with respect to fish weight did not show a clear tendency to increase, i.e. the investment in gonadal tissue does not increase in the larger size classes. The above-mentioned species have different life spans; the brown meagre lives longer than the porgy: porgy generally live to 10 years and older (Matsuyama *et al.,* 1987), while the brown meagre reaches at least 15 years of age and there is one record of a 22-year-old female (Chauvet, 1991). It may be that the different reproductive strategies adopted by these two species are related to their different life spans. The porgy increases its batch fecundity throughout its life, increasing gonadal investment in the larger size classes, while the brown meagre does not increase the proportions of the gonads with growth, relying instead on a longer life in which to reproduce. On the other hand, a morphological constraint could exist for the brown meagre, which may prevent it from being able to increase the gonadal investment. In this situation, the higher growth rate of females could be seen as a reproductive strategy to augment the proportion of the gonads.

Population composition

It is clear that our results have a higher percentage of larger size classes than those obtained by other authors (Chauvet, 1991; Dulčić and Kraljević, 1996; Chakroun-Marzouk and Ktari, 2003; Morey *et al.*, 2003). Our length frequency distribution is clearly skewed in favour of high size classes by the fishing methods employed: the spear fishing championships on the Balearic islands established a weight restriction of 300 g for brown meagre (29.1 cm TL), punishing the captures of fish below that threshold value, while our experimental fishing used a large mesh size (80 mm stretched mesh), which reduces the chance of capturing young individuals.

Deviations from a 1:1 sex ratio in larger size classes may suggest a sex change (Wenner, 1972), though our histological observation of gonads did not provide evidence of this. On the contrary, our histological data reveal that brown meagre is an iteroparous, gonochoristic, batch-spawning species with external fertilisation, as are all the studied members of the Sciaenidae (Francescon and Barbaro, 1999; Fennessy, 2000). According to Sadovy and Shapiro (1987), size differences between sexes could also be explained in a gonochoristic species by differential growth and longevity, differential migration or spatial segregation by sex. The difference in brown meagre growth rates (Chauvet, 1991; Chakroun-Marzouk and Ktari, 2003) and longevity between sexes (Chauvet, 1991) could explain this deviation. Others sciaenids from the coast of South Africa have the same growth differential pattern (Fennessy, 2000).

Our results reveal that in the Balearic Islands brown meagre attains sexual maturity at higher sizes: 25.4 cm TL (21.1 cm of SL) for males, 29.9 cm TL (25.1 cm of SL) for females. The only other estimate of size at maturity available for brown meagre was obtained from this species in Tunisian waters: 20 cm SL for males and 21 cm SL for females (Chakroun-Marzouk and Ktari, 2003). The larger size at maturity for brown meagre in this study could be related to the lower water temperature and higher latitude of Balearic Islands waters. Fish usually mature and spawn earlier in an environment with higher water temperature (Liu *et al.*, 2001), as is the case of Tunisian waters. Other differences in environmental conditions, food availability, quality of food resources and/or fishing pressure could also influence this difference in size at maturity as stock density, food, and water temperature may influence the growth of fish and further affect the age of first maturity (Tormosova, 1983).

In the Balearic Islands the brown meagre population exhibits a significant positive allometric growth for both individual sexes and the total population. Morey *et al.* (2003) also obtained the same results for total population (b= 3.254) in the same geographical zone. Comparison of our *b* values for the species with those obtained in Croatian (b=3.048; Dulčić and Krajelvić, 1996) and Tunisian waters (b=2.81; Chauvet, 1991; b males= 3.016, b females=2.975; Chakroun-Marzouk and Ktari, 2003) suggests that there are inter-regional differences. However, these differences may also be due to sampling differences as there are large differences in the number of speci-

mens and sampled length range among localities due to our sampling bias in favour of adults. While this may have influenced our results, as juveniles tend to be more isometric than breeders, which could result in an overestimation of brown meagre allometric growth, a comparison between the two more complete sampled populations from Tunisian (12.4-52.5 cm TL; Chauvet, 1991) and Balearic waters (14.2-58.2 cm TL: Morey *et al.*, 2003) also reveals the same biological trend of positive allometric growth in Balearic waters and negative allometric growth in Tunisian waters. This suggests that geographical variation in WLR may be real, as has been previously shown in other species (Sparre *et al.*, 1989; Mommsen, 1998).

HSI and energy status

Liver size of brown meagre varied little in both sexes. In females it ranged between a high of 2.04 in May to low of 0.98 in August, with the relative mean weight of vacuolised livers being no different to that of non-vacuolised livers. The vacuolised livers of both sexes did not differ either. Moreover, brown meagre specimens with higher HSI levels have livers with a moderate lipid droplet content, and migration of the liver cell nucleus and the presence of a unique (or two) enormous vacuole ("ring cells") characteristic of a great lipid accumulation (Rueda-Jasso *et al.*, 2004) were not observed. In fishes such as members of the family Gadidae, where the liver acts as the main lipid store, the liver index (HSI) is well correlated with the lipid content of the liver, and the HSI exhibits dramatic variations according to the energy status of the fish (Jensen, 1979; Lambert and Dutil, 1997). On the other hand, in the red drum, another benthic sciaenid, lipid reserves are distributed between the liver and mesenteric fat, with mesenteric lipid reserves being greater for most of the year (Craig *et al.*, 2000). Therefore, it seems that HSI is not a very good indicator of total lipid reserves of brown meagre, which can be distributed among other reservoirs.

The brown meagre has been included in the Red Data Book of Balearic Islands fishes under the category of species threatened by spear fishing and trammel nets (Mayol *et al.*, 2000). Moreover, its moderate longevity (15-21 years, Chauvet, 1991) indicates that the species may be vulnerable to overexploitation (Hutchings *et al.*, 2006). In spite of this there is no minimum legal length for captures of this

species in Balearic waters, with the exception of some marine reserves in which the minimum legal size is 34.5 cm TL. It therefore seems advisable that current management measures, which are clearly inappropriate, should be re-evaluated in the near future, and that stock assessment and management of Balearic brown meagre should take into account the reproductive biology information presented in this paper. We propose a minimum legal length of 30 cm TL based on female size at maturity obtained in this study (29.9 cm of TL), and the establishment of a fishing prohibition from May to July based on GSI and spawning activity data, in order to allow most females to have the possibility to spawn and thus ensure some offspring.

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