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## The reproductive biology of *Diplodus sargus sargus* in the Gulf of Tunis (central Mediterranean)

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**SUMMARY:** The sexual activity of *Diplodus sargus sargus* in the Gulf of Tunis takes place from January to May. Spawning occurs in spring (March to May), as the water temperature rises from 15 to 18°C, just after the winter minimum. The spawning period increases as the latitude decreases. The overall male to female ratio was statistically different from unity. Size at sexual maturity (TL<sub>50</sub>) was 21 cm (4 years old). The length-weight relationship for all individuals was described by the following parameters: a = 0.015 and b = 3.051. *D. s. sargus* from the Gulf of Tunis is a rudimentary hermaphrodite with partial protandry.

**Keywords:** *Diplodus sargus*, reproduction, hermaphroditism, protandry, length-weight relationship, Tunisia.

**RESUMEN:** BIOLOGÍA REPRODUCTIVA DE *DIPLODUS SARGUS SARGUS* EN EL GOLFO DE TÚNEZ (MEDITERRÁNEO). – La actividad sexual de *Diplodus sargus sargus* del golfo de Túnez tiene lugar de enero a mayo. La puesta tiene lugar en primavera (marzo a mayo), cuando la temperatura del agua sube de 15 a 18°C, justo tras el mínimo invernal. A medida que la latitud decrece se observa un periodo reproductivo progresivamente más extenso. La relación machos/hembras fue significativamente distinta de uno. La talla de madurez sexual (TL<sub>50</sub>) fue 21 cm (4 años). La relación talla-peso para todos los individuos se describió por los siguientes parámetros: a = 0.015 y b = 3.051. *D. s. sargus* del golfo de Túnez es un a hermafrodita rudimentario con proterandria parcial.

**Palabras clave:** *Diplodus sargus*, reproducción, hermafroditismo, proterandria, talla-peso, golfo de Túnez.

### INTRODUCTION

The white sea bream, *Diplodus sargus sargus* (Linnaeus, 1758), is one of the five species of *Diplodus* found in Tunisia. It shows a high polymorphism in all of its distribution areas with no fewer than seven subspecies (Paz *et al.*, 1973; Paz, 1981; Bauchot and Hureau, 1986; Abou-Seedo *et al.*, 1990). It inhabits the littoral zone in shallow waters down to 50 m; the juveniles occupy shallow sandy bottoms, whereas adults prefer deeper rocky areas covered by seaweed (Quéro and Guéguen,

1978; Harmelin-Vivien *et al.*, 1995; Sala and Ballesteros, 1997; Macpherson, 1998; Vigliola *et al.*, 1998; Vigliola and Harmelin-Vivien, 2001). *D. sargus* is also reported in ponds (Quignard and Man-Wai, 1983).

Sparidae are a highly valuable commercial family in Tunisia, representing nearly 7.4% by value of total catches for this region (Anonymous, 2001). The Sparidae species show all kinds of hermaphroditism: simultaneous, sequential and rudimentary, the latter also being called “late” gonochorism (Buxton and Garrat, 1990). This diversity is pre-

sumably linked to the bipotential aspect of all Sparidae gonads (D'Ancona, 1949 and 1950). It is therefore essential to determine the reproductive style of each sparid species in order to obtain a better understanding of its biology, a suitable evaluation of its population dynamics and a good management of its fisheries.

The aim of our work was to provide some preliminary information on the modality of sexual expression and reproductive characteristics exhibited by the white sea bream of the Gulf of Tunis: sex ratio, length-weight relationship, sexual cycle, spawning period, hepatic and muscular energy reserve changes and length at first sexual maturity. We compare our results with those available from other regions: the Italian (Lissia-Frau, 1968) and Egyptian coasts (El Maghraby *et al.*, 1981a, 1981b and 1982) and the Gulf of Lions (Man-Wai and Quignard, 1984; Man-Wai, 1985). Data are also available in the Persian Gulf for *D. sargus kotschy* (Abou-Seedo *et al.*, 1990), in northern Spain and the Azores for *D. sargus cadenati* (Martinez and Villegas, 1996; Morato *et al.*, 2003), and in South Africa for *D. sargus capensis* (Mann and Buxton, 1998).

## MATERIALS AND METHODS

Samples were collected on a monthly basis between September 2002 and February 2004; 223 white sea breams (TL = 11.2 to 34.2 cm) were fished by gillnets in the Gulf of Tunis and 24 specimens (TL = 25.9 to 37.2 cm) were spearfished off the Cani Island coast (GPS points: between 37°21'N, 10°07'E and 37°20'N, 10°07'E) at depths ranging from 15 to 25 m (Fig. 1). All these fishes (n = 247) were gathered in this study.

In the laboratory, for each specimen total length (TL) was measured to the nearest mm. Total (TW) and eviscerated weights (EW) were recorded to the nearest g, and gonads (GW) and liver (LW) weights were noted to the nearest 0.01 g.

Multiple mean length comparisons were performed with the Kruskal-Wallis test, followed by a Student-Newman-Keuls nonparametric (SNK) test after null hypothesis rejection (Zar, 1999).

Sexes were distinguished after macroscopic observation of gonads. The fishes were considered as immature (I) if they had no clearly identifiable sex; males (M) if they had only testes and females

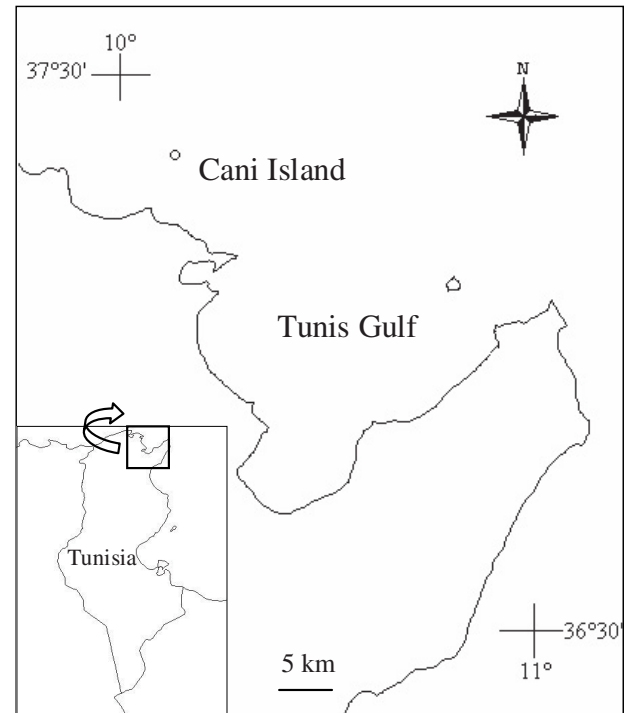


FIG. 1. – Map of the sampling areas (Gulf of Tunis and Cani Island).

(F) if they had only ovaries. Individuals were considered as hermaphrodites when male and female parts of the gonads occurred in equal or different proportions: Mf: male tissue was predominant, Fm: female tissue was predominant, MF: male and female tissues occurred in equal proportions.

The parameters of the total length-weight relationship ( $TW = aTL^b$ ),  $a$  and  $b$ , and the coefficient of determination ( $r^2$ ) were estimated over the entire period by least squares regression using the log transformed weights and sizes. According with Ricker (1973), the slope of the regression was corrected to follow a geometric mean regression. An ANCOVA test was used to compare regression lines between sexes and a t-test to test the isometry of growth ( $H_0$ : slope = 3;  $H_1$ : slope >3) (Zar, 1999).

Gonads were visually assessed for their stage of maturation according to Mann and Buxton (1998). We adopted this scale owing to the similarities observed concerning the gonads' appearance during the different periods of the sexual cycle: Stage 1, inactive (very thin translucent tubes); Stage 2, developing (ovaries are swollen with orange tubes, eggs are visible to the naked eye, testes show some thickening and are white); Stage 3, ripe (ovaries are very large, translucent eggs are visible, testes are very large and white, sperm is found in the testicular tis-

sue and the main sperm duct); and Stage 4, post-spawning (ovaries are flaccid, bloodshot and small in size, testes are smaller in size and pinkish-grey in colour).

The numeric proportions of sexes were expressed as male and female percentages and also as a male:female ratio, and were compared with a balanced sex-ratio (1:1) with a  $\chi^2$  test. The length at first sexual maturity was estimated for the males, females and pooled sexes from fishes collected only during the gonad maturation period. The proportion of mature individuals was fitted by the following logistic function:

$$P = 1 / (1 + e^{-b(TL - TL_{50})})$$

where P is the proportion of mature fish for the length TL, b is the slope of the maturity curve, and  $TL_{50}$  is the size at which 50% of the fish are mature. We considered as mature individuals whose gonads were consistent with Stages 2, 3 and 4 of the above gonad maturation scale. Multivariate analysis (Hotelling's  $T^2$  test) was used to compare the logistic model parameter estimates for males and females (Bernard, 1981).

We estimated age at first maturity for the pooled sexes after reading the scales of white sea breams corresponding to  $TL_{50}$  size class and those of the lower and higher size classes. Taking into account that the birth date was in March (see results) and that the growth recovered each year after the winter break, i.e. in March, we considered that one annulus corresponded to one year.

The reproductive period was determined by analysing the monthly variation in the gonad maturity stages as well as the gonadosomatic index ( $GSI = GW / EW \times 100$ ). Correlation between GSI and temperature was tested using the Spearman rank correlation coefficient ( $r_s$ ) (Zar, 1999). Moreover, the fluctuations of lipid reserves in the liver and the muscles were observed by monitoring respectively the monthly hepatosomatic index ( $HSI = LW / EW \times 100$ ) and condition factor ( $CF = EW / TL^3 \times 100$ ) (Anderson and Gutreuter, 1983).

The mean sea water temperature data were supplied by the National Institute of Meteorology.

To determine the sexual typology of hermaphroditism, we took into account and compared, for each sex, the length frequency distribution, mean size and mean GSI, as recommended by Buxton and Garrat (1990). The method of Shapiro (1984), which con-

sists in aggregating the length frequency distribution where females and males overlap and then calculating the median of the distribution, was used to calculate the sexual inversion length.

With the sole aim of detecting whether there were signs of sexual inversion, we performed a histological examination of the gonads of 32 white sea breams selected randomly from the full size range (15.8 to 37.2 cm) and for each period (resting, developing, ripe and post-spawning). Sub-samples of gonadic tissues were fixed in Bouin's solution for 2-3 days and then dehydrated before being embedded in paraffin wax; after cutting, transverse sections of 6  $\mu$ m width were stained with eosin and toluidin blue.

## RESULTS

### Structure of the population

Our sample was composed of 92 immature fishes (TL: 11.2 to 19.3 cm), 108 females (TL: 15.5 to 37.2 cm), 37 males (TL: 15.8 to 30.0 cm), and 10 hermaphrodites (TL: 17.6 to 33.6 cm). The mean length of immature fishes ( $TL = 14.6 \pm 0.2$  cm) was significantly lower (Kruskal-Wallis test,  $n = 237$ ,  $p < 0.001$ ) than that of males ( $TL = 21.7 \pm 0.6$  cm) (SNK,  $p < 0.05$ ) and females ( $TL = 23.8 \pm 0.5$  cm) (SNK,  $p < 0.05$ ). Male and female mean lengths were not significantly different (SNK,  $p > 0.05$ ) (Fig. 2).

Length-weight regression parameters estimated for males, females and all individuals are presented in Table 1. The length-weight relationships were significant (ANOVA,  $p < 0.001$ ) in the three different groups. However, there were no statistically significant differences in slopes or intercepts between males and females (ANCOVA,  $n = 145$ ,  $p > 0.05$ ).

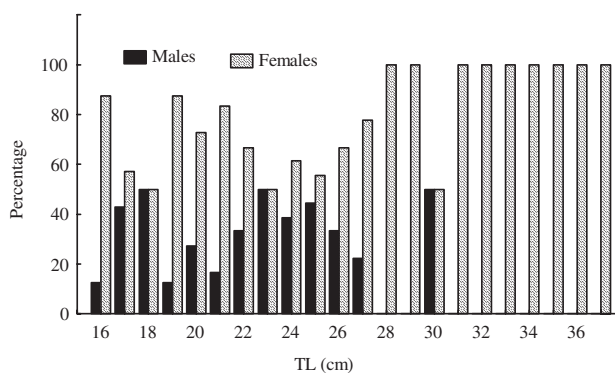


FIG. 2. – Length-frequency distribution of females and males of *Diplodus sargus sargus*.

TABLE 1. – Parameters of the length-weight relationships for females, males and all fish (males, females, immatures and hermaphrodites) of *Diplodus sargus sargus* in the Gulf of Tunis. All the 3 relationships were significant (ANOVA,  $p < 0.001$ ). The isometry was tested by Student's t-test ( $H_0: t = 3$ ). a: intercept, b: slope, s.e. (b): standard error of b, n: sample size,  $r^2$ : coefficient of determination.

	a	b	s.e. (b)	n	$r^2$	t-test	p
Males	0.012	3.129	0.098	37	0.983	1.323	0.19
Females	0.018	2.994	0.050	108	0.985	0.119	0.90
All fish	0.015	3.051	0.024	247	0.984	2.119	0.03

TABLE 2. – Percentage and sex ratio of *Diplodus sargus sargus* males and females according to the different sexual cycle periods in the Gulf of Tunis.

Periods	% M	% F	Sex ratio (M : F)	$\chi^2$	P
Sexual activity period (December to June)	40.63	59.37	1 : 1.46	2.25	>0.05
Resting period (July to November)	17.74	82.26	1 : 4.64	25.08	<0.05
Overall ratio	29.37	70.63	1 : 2.92	21.46	<0.05

The female and male growths were isometric (t-test,  $p = 0.19$  and  $0.90$  respectively) but positively allometric for pooled individuals ( $p = 0.03$ ).

**Sex ratio, length and age at first maturity**

The overall ratio of males to females (1: 2.92) was clearly in favour of females ( $\chi^2$ ,  $n = 126$ ,  $p < 0.05$ ) and, whatever the size class, females were always significantly more numerous than males (all  $\chi^2$ ,  $p < 0.05$ ). From December to June, the sex ratio was balanced ( $\chi^2$ ,  $n = 64$ ;  $p > 0.05$ ), but from July to November females were more numerous than males ( $\chi^2$ ,  $n = 62$ ,  $p < 0.05$ ; Table 2).

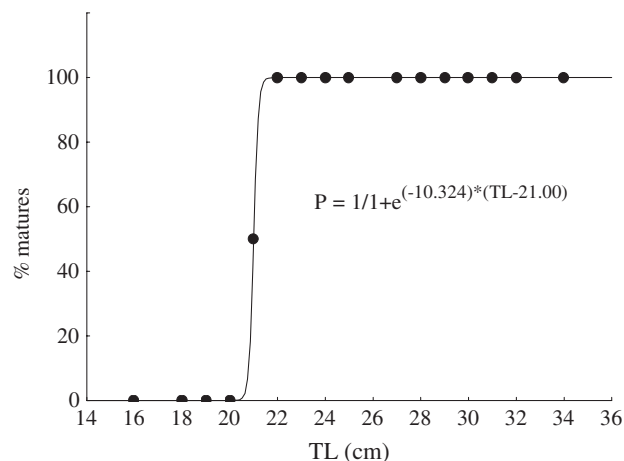


FIG. 3. – Maturity ogive of *Diplodus sargus sargus*.

Size at 50% maturity was attained for males and females at 20.5 cm (s.e.  $< 0.001$ ,  $n = 22$ ) and 21.4 cm TL (s.e.  $< 0.001$ ,  $n = 27$ ), respectively; no significant difference in length at first maturity was found between sexes (Hotelling's  $T^2$  test, d.f. = 25,  $T = 2.562$ ,  $p < 0.05$ ). The sexual maturity ogive for the pooled sexes yielded a length at first sexual maturity of 21 cm (Fig. 3); according to the scale reading of the concerned length classes, this size corresponds to an age of 4 years. Among the 247 sampled fish, 59.5% did not reach the first maturity length.

**Sexual cycle**

During the gonad maturation period, the mean testis weight ( $8.10 \pm 2.34$  g) was not significantly different (Mann-Whitney test,  $n = 33$ ,  $p = 0.41$ ) from the ovarian one ( $11.18 \pm 3.12$  g). Monthly mean GSI ranged from 0.01 to 4% for males ( $1.22 \pm 0.42\%$ ) and from 0.07 to 4.94% for females ( $1.01 \pm 0.41\%$ ); these two values were not significantly different (Wilcoxon test,  $n = 12$ ,  $p = 0.75$ ).

The curves of the GSI monthly values were unimodal for both males and females, so *D. s. sargus* reproduced only once a year (Fig. 4). The durations of the male and female gonad development were similar, with a resting period from July to November. The male gonadic activity started in December and reached a maximum in February and March. The female gonadosomatic index was highest in March, one month later than males. The spawning period started in March, and in May or June the majority of fishes were post-spawners. Significant correlation was found between mean

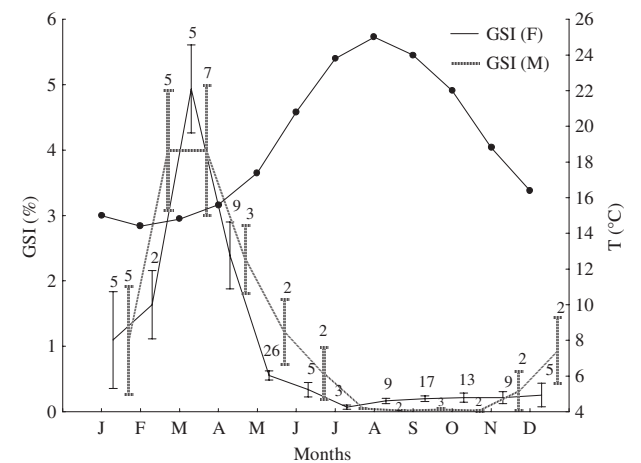


FIG. 4. – Monthly mean  $\pm$  s.e. gonadosomatic index for mature males (M) and females (F) and of the mean temperature of sea water ( $T^\circ\text{C}$ ) in the Gulf of Tunis. (Temperature data supplied by the National Institute of Meteorology).

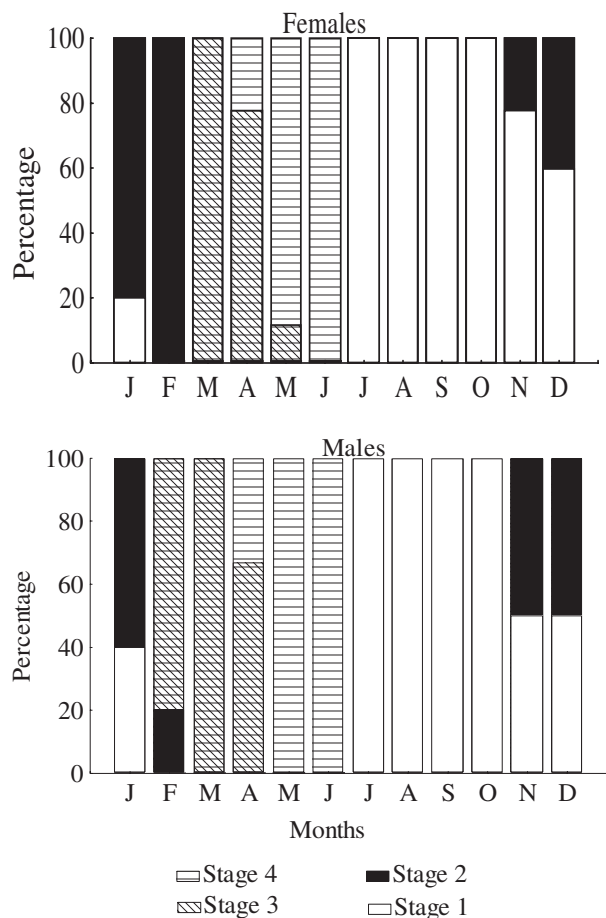


FIG. 5. – Maturity stages of males and females of *Diplodus sargus sargus*. Stage 1: resting, Stage 2: developing, Stage 3: ripe, Stage 4: post-spawning.

GSI values and sea surface temperature ( $r_s = -0.916$ ,  $n = 12$ ,  $p < 0.05$ ). The complete gonad maturation occurred at the lowest sea surface temperatures (from 14 to 16°C; Fig. 4)

The monthly succession of gonad maturity stages 1 to 4 (Fig. 5) confirmed the yearly GSI fluctuation (Fig. 4). From July to October, only stage 1 (gonad in resting stage) was observed; stages 2 and 3 (ripe gonads) were observed from February to April (males) or March to May (females), and stage 4 from April to June (both sexes).

The monthly mean condition factor fluctuated from 1.46 to 1.81% ( $1.65 \pm 0.01\%$ ) for males and from 1.52 to 1.72% for females ( $1.61 \pm 0.01\%$ ). The mean condition factors were not significantly different between sexes (Mann-Whitney test,  $n = 12$ ,  $p = 0.18$ ). For all mature fishes (males, females and hermaphrodites), the condition factor was significantly different between months (Kruskal-Wallis test,  $n = 155$ ,  $p = 0.001$ ), being highest in summer and lowest in April (SNK,  $p < 0.05$ ).

The monthly mean hepatosomatic index ranged from 0.87 to 1.54% ( $1.16 \pm 0.02\%$ ) for males and from 0.66 to 1.13% ( $0.92 \pm 0.03\%$ ) for females. The mean HSI was different between sexes (Mann-Whitney test,  $n = 12$ ,  $p = 0.03$ ). HSI means for males and females were not significantly different between months (Kruskal-Wallis test,  $n = 12$ ,  $p = 0.36$  and 0.12, respectively)

### Hermaphroditism

The observation of gonads with naked eyes showed a small number of bisexual gonads (6.4%), suggesting that *D. s. sargus* is hermaphroditic. These hermaphroditic fishes were mainly observed in June, the post-spawning period. Most of the time the gonads showed one sex as being more developed than the other, with a higher mean total length for the individuals with a more developed ovary (1 Mf: TL = 18.4 cm; 1 MF: TL = 22.5 cm; 8 Fm: TL =  $27.1 \pm 2.1$  cm). However, the mean total length of

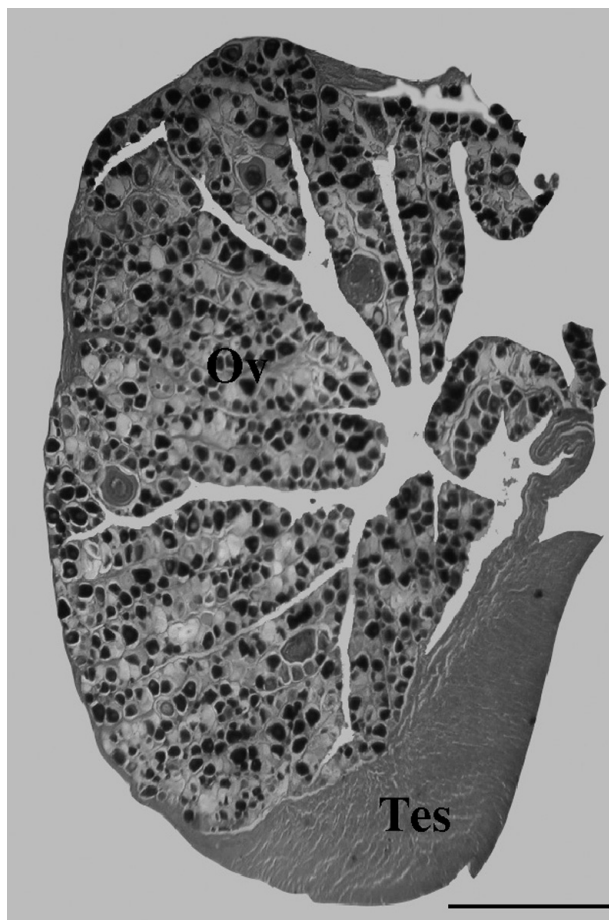


FIG. 6. – Transverse section of *Diplodus sargus sargus* gonad betraying sexual inversion, TL = 19.4 cm, June; Ov: ovary, Tes: testis. Scale bars = 0.5 mm.

the hermaphrodites as a whole ( $TL = 25.7 \pm 1.9$  cm) was not significantly different from that of females and males (Kruskal-Wallis test,  $n = 155$ ,  $p = 0.11$ ). Sexual inversion took place at approximately 22 cm, this being the median distribution of 123 individuals ranging in size from 15.8 to 30.0 cm.

The histological study of random gonad sub-samples showed that, in fact, all fishes showed bisexual gonads. Within an ovotestis, the relative size of each germinal territory was not sufficient to consider whether an individual was a functional male or female or a juvenile. For example, outside the sexual activity period, the ovary may be bigger than the testis in a great number of functional males and juveniles and yet a lot of these fishes will function as males during the next spawning season. For these reasons, the number of males of the smallest size classes could have been underestimated. However, the histological study of a small sub-sample allowed us to identify a single gonad undergoing sexual inversion (Fig. 6) and that was a real experimental indicator of sex change. It consisted of a developed ovarian portion containing pre-vitellogenic oocytes and a testicular portion in regression within which some residual spermatozooids betrayed a previous functional testis. Otherwise, bisexual gonads with two well-proportioned territories were very scarce, so the transitory phase of sexual inversion seems to be rather short.

## DISCUSSION

### Reproductive seasonality and biophysiology

In the Gulf of Tunis, the sexual activity of *D. s. sargus* started in January and continued through June; spawning extended from March to May with a peak in March-April. As the latitude decreased (Table 3), the spawning period started earlier and its

duration increased from 3 to 5 months. These regional dissimilarities have already been noticed and correlated with changes in thermal regimes (Morato *et al.*, 2003). A longer spawning period also indicates that favourable environmental conditions for hatching and larval development are available for a longer period (Gonçalves and Erzini, 2000). It is well known that the sexual activity and the duration of spawning are governed by temperature and photoperiod. In the Gulf of Tunis, *D. s. sargus* spawning started as sea temperature increased after the winter minimum, as had been also recorded in the Azores (Morato *et al.*, 2003).

The male GSI reached the maximum one month before that of the female, which may be due to a competition strategy between males (Sousa *et al.*, 2003). This hypothesis is supported by several authors, who reported that *D. sargus* males compete with each other to fertilise eggs (Buxton and Garratt, 1990; Gonçalves and Erzini, 2000).

*D. sargus* from the Azores have a good condition factor during both spawning and post-spawning periods (Morato *et al.*, 2003). Similarly, the condition factor of *D. sargus* from the northwestern Mediterranean (Lloret and Planes, 2003) and from Egypt (El Maghraby *et al.*, 1982) does not differ between maturity stages. However, subsequent to spawning, a slimming of the white sea breams from the Lion Gulf has been reported (Man-Wai, 1985). A peri-intestinal lipid utilisation during the production and emission of gametes has also been observed for *D. sargus* from the north of Spain (Martinez and Villegas, 1996). In this study, the white sea bream condition factor in the Gulf of Tunis seemed to be affected by sexual activity but the hepatosomatic index did not show statistical differences between months.

The role of liver reserves during reproduction is not clear, and other methods are needed in order to determine whether hepatic reserves are mobilised

TABLE 3. – Period and duration of *Diplodus sargus* spawning according to the latitude. t: sea water temperatures during the spawning period.

Authors	Region	Latitude	Spawning period	Spawning duration (months)	t (°C)
Man-Wai (1985)	Gulf of Lion, France	43°N36	April - May	3	
Martinez and Villegas (1996)	Asturias, Spain	43°N	April - June	3	13-17
Morato <i>et al.</i> (2003)	Azores, Portugal	38°N	March - June	4	15-17
Present study	Gulf of Tunis, Tunisia	36°N48	March - May	3	15-18
El Maghraby <i>et al.</i> (1982)	Egyptian coasts	31°N12	January - April	4	
Abou-Seedo <i>et al.</i> (1990)	Kuwait	29°N	November - March	5	
Mann and Buxton (1998)	South African coasts	34°S	August - March	8	17-20

for gonad maturation or the energy stored in the liver is channelled to muscular activity.

### Length and age at first maturity

The length at first maturity of the Gulf of Tunis white sea bream (21 cm) was similar to that reported in the north of Spain (21 cm) (Martinez and Villegas, 1996), lower than in South Africa (24.3 cm) (Mann and Buxton, 1998) and the Lion Gulf (23 cm for females and 20 cm for males), and higher than in the Azores (16.7 cm) (Morato *et al.*, 2003) and Egypt (18 cm) (El Maghraby *et al.*, 1982). The *D. s. sargus* population of the Gulf of Tunis appears to be distinguishable from the others by its late maturity (4 years); the Azores population has a maturity of 2 years (Morato *et al.*, 2003), whereas the populations of northern Spain (Martinez and Villegas, 1996) and the South African coasts (Mann and Buxton, 1998) have a maturity of 3 years. These inter-population variations in age and length at first maturity are probably linked to growth differences of populations, the growth being affected by environmental factors such as temperature, food quality and availability, demographic structure and selective predation by size (Duponchelle and Panfili, 1998).

In addition, if the length composition of our sample reflects the commercial fishery catches in the Gulf of Tunis, we must point out that about 60% of the fish caught were smaller than length at first maturity. Therefore, in order to improve the stock management of *D. s. sargus* and the conservation of this species in the Gulf of Tunis, an increase in the minimum legal length authorised for capture is strongly recommended.

### Population structure, reproductive style and behaviour

In the Gulf of Tunis, the proportion of hermaphrodites was very low when fishes were sexed from the macroscopic appearance of gonads (6.4%) but considerably higher after histological sexing (81.2%). In northern Spain, a 5.6% of hermaphrodites were found after macroscopic sexing (Martinez and Villegas, 1996), which was close to our results in Tunisia. Combining the two methods of sexing, hermaphrodites accounted for 23% of *D. sargus* along the Egyptian coasts (El Maghraby *et al.*, 1981a) and 50% in the Gulf of Lions (Man-Wai, 1985). The estimated hermaphrodite fraction for the various white

sea bream populations is therefore broadly dependent upon the methods used by the different authors to determine sex. However, it is known that the gonads of Sparidae are all bisexual from an early development stage (D'Ancona, 1946), which is why, in our opinion, microscopic sexing leads to a higher percentage of hermaphrodites. This bipotentiality is considered as a pre-adaptation for the development of a sequential hermaphroditism in species in which reproductive success is size-related (Buxton and Garrat, 1990). In this case, individuals maximise lifetime reproductive success by functioning as one sex when small and as the other when large in accordance with "the size advantage model" (Ghiselin, 1969). Other Sparidae do not agree with this expectation and exhibit a rudimentary hermaphroditism in which young fish possess an immature intersexual gonad but mature as either males or females with no evidence of sex reversal (Buxton and Garrat, 1990). Distinctive features have thus made it possible to characterise sequential and rudimentary hermaphrodites (Buxton and Garrat, 1990): in sequential hermaphroditic species, the male and female mean sizes and gonadosomatic indices are significantly different and their size frequencies are bimodal; in rudimentary hermaphroditic species, sexes have similar mean sizes and gonadosomatic indices, and their length frequency distributions overlap.

In the Gulf of Tunis, *D. s. sargus* males and females showed overlapping length frequency distributions, although the females dominate the larger size classes. The mean gonadosomatic indices did not differ between sexes. According to the two reproductive styles defined above, the *D. s. sargus* population of the Gulf of Tunis showed a rudimentary hermaphroditism with a partial protandry. This hypothesis is reinforced by our prospective histological study: (1) the gonads of the smallest males and females were non-functional intersexual gonads (primary males and females); (2) though sporadically, we detected gonads in sexual inversion, revealing the transformation of some protandrous males into secondary post-mature females. A supplementary argument supporting the partial protandry hypothesis is that the overall Gulf of Tunis white sea bream population had three times more females than males. Our conclusions confirm the assumptions expressed by studies carried out in the Mediterranean on *D. sargus sargus*: as previously reported, this subspecies shows a rudimentary hermaphroditism with a facultative protandry (D'Ancona, 1949; Tortonèse, 1965; Lissia-Frau,

1968; Man-Wai, 1985). Even in captivity, an optional protandry is argued (Micale and Perdichizzi, 1994). For all others subspecies—*D. sargus capensis* of South Africa, *D. sargus kotschy* of the Persian Gulf and *D. sargus cadenati* of northern Spain and the Azores—the observation of both primary and secondary females is explained by digyny (Buxton and Garrat, 1990; Mann and Buxton, 1998).

In the Gulf of Tunis, *D. s. sargus* sex ratio fluctuations indicated a sex separation outside the breeding season and a sex gathering for spawning; the same behaviour has been already noticed but for a congeneric species, *D. vulgaris* (Man-Wai, 1985; Gonçalves and Erzini, 2000). Schooling (Macpherson, 1998) and an equal size of sexes have favoured the selection of mating behaviour such as random mating between pairs and group spawning, both within spawning aggregations (Buxton and Garrat, 1990). This life-history, characterising rudimentary hermaphrodites Sparidae, has also been observed for the rudimentary hermaphrodites Labridae with a poorly organised social system (Michel *et al.*, 1987). The question then is to determine the main factors that would favour a sexual inversion of some individuals within a rudimentary hermaphrodite population. In an optional sequential hermaphroditism, the potential of some fishes to change sex most probably depends on social factors such as demographic or behavioural deterioration or on environmental factors such as temperature or insufficient nutrition (D'Ancona, 1950; Warner, 1975 and 1988; Alekseev, 1983; Buxton and Garrat, 1990), rather than on a genetic predetermination (Lenfant, 2002). Indeed, the assumption that sex change in fish is genetically predetermined is therefore not sufficient to explain its intermittent occurrence among *Diplodus*.

The length and age of sexual inversion of different white sea bream sub-species populations can be seen to be different: protandrous sex change for *D. s. kotschy* from Kuwait bay occurs during their second year of life (Abou-Seedo *et al.*, 1990), whereas in northern Spain some *D. s. cadenati* males change sex during their fourth year of life, i.e. at 25 cm length (Martinez and Villegas, 1996). Gonads in sexual reversal have been found in *D. s. capensis* off the coast of South Africa at lengths ranging between 25 and 34 cm (Mann and Buxton, 1998), while for *D. s. sargus* from the Gulf of Tunis they have been found at lengths of 22 cm. The latest observation needs to be confirmed by a large-scale histological study of the whole population.

In conclusion, *Diplodus sargus* digyny seems to be confirmed for the whole distribution area of the species. Furthermore, even partial protandry results in a greater number of larger females that are potentially more fecund, which is beneficial in terms of spawning potential (Gonçalves and Erzini, 2000).

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## REFERENCES

- Anonymous. – 2002. Annuaires statistiques des produits de la pêche en Tunisie de 1995 à 2001. Direction Générale de la pêche et de l'Aquaculture du Ministère de l'Agriculture à Tunis.
- Abou-Seedo, F., J.M. Wright and D.A. Clayton. – 1990. Aspect of the biology of *Diplodus sargus kotschy* (Sparidae) from Kuwait bay. *Cybiium*, 14: 217-223.
- Alekseev, F.E. – 1983. Hermaphroditisme in Porgies (Perciformes, Sparidae). II. Sexual structure of the populations, mechanism of its formation and evolution in scups, *Pagrus pagrus*, *P. orphus*, *P. ehrenbergi* and *P. auriga*. *J. Ichtyol.*, 23(2): 61-73.
- Anderson, R.O. and S.J. Gutreuter. – 1983. Length, weight, and associated structural indices. In: Fisheries techniques. L. A. Nielsen and D. L. Johnson (eds). *Am. Fish. Soc.*, Bethesda, MD, pp. 283-300.
- Bauchot, M.L. and J.C. Hureau. – 1986. Sparidae. In P.J.P. Whitehead, M.L. Bauchot, J.C. Hureau, J. Nielsen and E. Tortonese (eds), *Fishes of the North-eastern Atlantic and the Mediterranean*, Vol. II, pp. 883-907. UNESCO.
- Bernard, D. – 1981. Multivariate analysis as a mean of comparing growth in fish. *Can. J. Fish. Aquat. Sci.*, 38: 233-236.
- Buxton, C.D. and P.A. Garratt. – 1990. Alternative reproductive styles in seabreams (Pisces: Sparidae). *Environ. Biol. Fish.*, 28: 113-124.
- D'Ancona, U. – 1946. Ermafroditismo e gonochorismo in alcuni Sparidi. *Boll. Soc. Ital. Biol. Sper.*, 12: 1-2.
- D'Ancona, U. – 1949. Il differenziamento della gonade e l'inversione sessuale degli Sparidi. *Arch. Oceanogr. Limnol.*, Anno VI Fascicola II-III : 97-163.
- D'Ancona, U. – 1950. Détermination et différenciation du sexe chez les poissons. *Arch. Anat. Micr. Morph. Exp.*, 39: 274-294.
- Duponchelle, F. and J. Panfili. – 1998. Variations in age and size at maturity of female Nile tilapia, *Oreochromis niloticus*, populations from man-made lakes of Côte d'Ivoire. *Environ. Biol. Fish.*, 52: 453-465.
- El Maghraby, A.M., G.A. Botros, M.T. Hashem, and E.A. Wassef. – 1981a. Hermaphroditism in three sparid fish, *Diplodus sargus* L., *Diplodus vulgaris*, Geoffr., and *Oblada melanura* L. from the Egyptian Mediterranean waters. *Bull. Inst. Oceanogr. Fish. ARE*, 7: 378-385.
- El Maghraby, A.M., G.A. Botros, M.T. Hashem, and E.A. Wassef. – 1981b. Age determination and growth studies of two sparid fish *Diplodus sargus*, L. and *Diplodus vulgaris*, Geoff. in the Egyptian Mediterranean waters. *Bull. Inst. Oceanogr. Fish. ARE*, 7: 386-394.
- El Maghraby, A.M., G.A. Botros, M.T. Hashem, and E.A. Wassef. – 1982. Maturation, spawning and fecundity of two sparid fish *Diplodus sargus*, L. and *Diplodus vulgaris*, Geoff. in the



- Egyptian Mediterranean waters. *Bulletin . Bull. Inst. Oceanogr. Fish. ARE*, 8: 51-67.
- Ghiselin, M.T. – 1969. The evolution of hermaphroditism among animals. *Q. Rev. Biol.*, 44: 189-208.
- Gonçalves, J.M.S. and K. Erzini. – 2000. The reproductive biology of the two-banded sea bream (*Diplodus vulgaris*) from the SW Coast of Portugal. *J. Appl. Ichthyol.*, 16(3): 110-116.
- Harmelin-Vivien, M.L., J.G. Harmelin, and V. Lebouleux. – 1995. Microhabitat requirements for settlement of juvenile sparid fishes on Mediterranean rocky shores. *Hydrobiologia*, 300-301: 309-320.
- Lenfant, P. – 2002. Hétérozygotie et valeur sélective : le cas du poisson marin, *Diplodus sargus* (Linné, 1758). *C. R. Biologies*, 325: 239-252.
- Lissia-Frau, A.M. – 1968. Le manifestazioni della sessualita negli Sparidi (Teleostei, Perciformes). *Studi Sassaressi*, 2: 243- 261.
- Lloret, J. and S. Planes. – 2003. Condition, feeding and reproductive potential of white seabream *Diplodus sargus* as indicators of habitat quality and the effect of reserve protection in the north-western Mediterranean. *Mar. Ecol. Prog. Ser.*, 248: 197-208.
- Macpherson, E. – 1998. Ontogenetic shifts in habitat use and aggregation in juvenile sparid fishes. *J. Exp. Mar. Biol. Ecol.*, 220: 127-150.
- Mann, B.Q. and C.D. Buxton. – 1998. The reproductive biology of *Diplodus sargus capensis* and *D. cervinus hottentotus* (Sparidae) off the south-east cape coast, South Africa. *Cybium*, 22: 31-47.
- Man-Wai, R. – 1985. Les sars du golfe du Lion, *Diplodus sargus*, *D. vulgaris*, *D. annularis* (Pisces, Sparidae). Ecobiologie, Pêche. Thèse de 3<sup>ème</sup> cycle, USTL Montpellier 361p.
- Man-Wai, R. and J.P. Quignard. – 1984. Les sars *Diplodus sargus* (Linné, 1758) du golfe du Lion: Croissance et caractéristique des débarquements aux criées de Sète et grau du Roi. *Rev. Trav. Inst. Pêches marit.*, 46: 173-194.
- Martinez, C. and M.L. Villegas. – 1996. Edad, crecimiento y reproducción de *Diplodus sargus* Linnaeus, 1758 (Sparidae) en aguas asturianas (norte de España). *Bol. Inst. Esp. Oceanogr.*, 12: 65-76.
- Micale, V. and F. Perdichizzi. – 1994. Further studies on the sexuality of the hermaphroditic teleost *Diplodus sargus*, with particular reference to protandrous sex inversion. *J. Fish Biol.*, 45: 661-670.
- Michel, Ch., P. Lejeune and J. Voss. – 1987. Biologie et comportement des Labridés européens (Labres, Crénilabres, Rouquiers, Vieilles et Girelles). *Rev. Aquariol.* 14: 80 pp.
- Morato, T., P. Afonso, P. Lourinho, R.D.M. Nash and R.S. Santos. – 2003. Reproductive biology and recruitment of the sea bream in the Azores. *J. Fish. Biol.*, 63: 59-72.
- Paz, R. de la – 1981. Note critique sur la nomenclature des *Diplodus* du groupe *sargus* (Pisces, Sparidae). *Bull. Mus. Natn. His. Nat. Paris*, 4: 931-934.
- Paz, R. M. de la, M.L. Bauchot and J. Daget. – 1973. Les *Diplodus* (Perciformes Sparidae) du groupe *sargus* : systématique et phylogénie. *Ichthyologia*, 5: 113-128.
- Quéro, J.C. and J. Guéguen. – 1978. Données sur la faune ichtyologique du golfe de Gascogne. 1. Répartition des *Diplodus* (Sparidae, Perciformes) et remarques sur leurs stades juvéniles. *Cybium*, 3: 82 - 94.
- Quignard, J.P. and R. Man-Wai. – 1983. Relations taille-poids et coefficient de condition de *Diplodus sargus* 0+ et 0++ de deux étangs palavasiens: Prévost et Mauguio. *Cybium*, 7: 31-41.
- Ricker, W.E. – 1973. Linear regressions in fishery research. *J. Fish. Res. Board Can.*, 30: 409-434.
- Sala, E. and E. Ballesteros. – 1997. Partitioning of space and food resources by three fish of the genus *Diplodus* (Sparidae) in a Mediterranean rocky infralittoral ecosystem. *Mar. Ecol. Prog. Ser.*, 152: 273-283.
- Shapiro, D.Y. – 1984. Sex reversal and Sociodemographic Processes in Coral Reef Fishes. In: G. W. Potts and R. J. Wootton (eds.), *Fish Reproduction: Strategies and Tactics*, pp. 103-117. Academic Press Limited, London.
- Sousa, L., J.P. Barreiros, M.S.C. Soares, M. Hostim-Silva and R.S. Santos. – 2003. Preliminary notes on the reproductive biology of the lizardfish, *Synodus saurus* (Actinopterygii: Synodontidae) in the Azores. *Cybium*, 27: 41-45.
- Tortonèse, E. – 1965. Biologie comparée de trois espèces méditerranéennes de *Diplodus* (Pisces Sparidae). *Rapp. P.V. Comm. Int. Explor. Sc. Me. Médit.*, 18: 189-192.
- Vigliola, L. and M.L. Harmelin-Vivien. – 2001. Post-settlement ontogeny in three Mediterranean reef fish species of the genus *Diplodus*. *Bull. Mar. Sci.*, 68: 271-286.
- Vigliola, L., M.L. Harmelin-Vivien, E. Biagi, R. Galzin, A. Garcia-Rubies, J.G. Harmelin, J.Y. Jouvenel, L. Le Direach-Boursier, E. Macpherson and L. Tunesi. – 1998. Spatial and temporal patterns of settlement among sparid fishes of the genus *Diplodus* in the northwestern Mediterranean. *Mar. Ecol. Prog. Ser.*, 168: 45-56.
- Warner, R.R. – 1975. The adaptive significance of sequential hermaphroditism in animals. *Amer. Nat.*, 109: 61-81.
- Warner, R.R. – 1988. Sex change in fishes: hypotheses, evidence, and objections. *Environ. Biol. Fish.*, 22: 81-9.
- Zar, J.H. – 1999. *Biostatistical Analysis*. Prentice-Hall, River, New Jersey.

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