

## The reproductive biology of *Spondyliosoma cantharus* (L.) from the SW Coast of Portugal\*

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**SUMMARY:** The study of *Spondyliosoma cantharus* (L.) reproduction was carried out within the framework of a project on the fisheries resources of the south-west coast of Portugal, and was based on the analysis of the spawning season, gonad maturation, size-at-maturity, fecundity, and hermaphroditism. Spawning took place from February to April, peaking in March. Analysis of the sex ratio by size class and season showed that females were more abundant throughout the year ( $M/F=0.57$ ) and in the smaller size classes. Overall size at first maturity ( $L_{50}$ ) was 20.10 cm total length (TL), with a significant difference between males (22.41 cm, TL) and females (19.98 cm, TL). Absolute fecundity (Fa) ranged from 37,506 to 112,074 oocytes, with a mean of 61,396. A power type relationship best described the relationships between absolute fecundity and TL ( $Fa = 436.27TL^{1.575}$ ), and somatic weight ( $Fa = 2979.7SW^{0.585}$ ). The number of oocytes/g of female somatic weight ranged from 217 to 549, with a mean of 346. The reproductive strategy of this species is characterised by protogynic hermaphroditism, as indicated by the presence of individuals in transition and of testes with vestiges of preceding ovaries associated with the significant differences in the size frequency distributions of the sexes.

**Key words:** reproduction, hermaphroditism, fecundity, Sparidae, *Spondyliosoma cantharus*, Portugal.

### INTRODUCTION

The black sea bream, *Spondyliosoma cantharus* (L.), choupa in Portuguese, is one of the commercially important sparids of the SW Coast of Portugal. Sparidae account for 5% and 21% of the landings by weight and value, respectively, in the Algarve (southern Portugal) (DGPA, 1997). Within this region, *S. cantharus* is targeted by gill nets, fish traps, and longlines using small hooks, and accounts for 22.7% of the catches of the latter gear (Erzini *et al.*, 1997).

To improve our understanding of the biology and the population dynamics of sea breams, and to contribute to better fisheries management, it is neces-

sary to take into account the complex expressions of hermaphroditism, including protandry, protogyny, and rudimentary hermaphroditism exhibited by these species. Information on reproductive aspects of *Spondyliosoma cantharus* has been reported by D'Ancona (1949), Wilson (1958), Perodou and Nedelec (1980), Soletchnik (1983), Lozano *et al.* (1990), Balguerías *et al.* (1993) and Dulčić *et al.* (1998).

The current study was carried out on the SW Coast of Portugal as part of a base-line study of the fishery resources in this area (Canário *et al.*, 1994). The aim of this study was to describe *S. cantharus* reproductive features and strategies, including spawning season, sex ratio, length at first maturity, hermaphroditism and fecundity, along with a comparison with other hermaphroditic sparids.

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## MATERIALS AND METHODS

This study was based on a monthly sampling program from December 1992 through March 1994, from the landings of the inshore artisanal fishery based in Sagres, Portugal (Fig. 1). The sampled fleet is characterised by small inshore boats with one or two fishermen using a small hook longline (hook size n°13, “Mustad” brand) of approximately 1200-1300 hooks baited with squid (*Loligo* sp.).

A total of 368 *S. cantharus* were collected randomly from the longline fleet. The samples were immediately transported to the laboratory where the following were recorded for each individual fish: total length (TL; to the nearest lower 0.5 cm); total weight (TW;  $\pm 0.01$ g); eviscerated weight (EW;  $\pm 0.01$ g); sex (visual and compound microscope evaluation of general characteristics); state of maturity (determined by macroscopic evaluation when possible, based on the maturity scales presented in Table 1) and gonad weight (GW;  $\pm 0.01$ g). The accuracy of macroscopic stages was assessed by histological analysis.

The gonadosomatic index (GSI = gonad weight / eviscerated weight)  $\times 100$ ) was calculated. The monthly trend for mean GSI values and the proportion of spawning specimens (maturity stages V for males and VI for females) over a 16 month period were used to determine the spawning season for the SW Coast of Portugal. The spawning season was established as the period during which the highest values of the GSI coincided with the highest percentages of sexually mature individuals. The start of the spawning season was compared with two environmental variables: sea surface temperature (SST) and the number of hours of day light.

The sex ratio (ratio of the number of males to females) and sex proportion by length class intervals (0.5 cm) were determined on a monthly basis. Monthly sex ratios were tested using the Kolmogorov-Smirnov test for significant differences from an expected ratio of 1:1 (Siegel and Castellan, 1988). A comparison of mean length values between sexes was carried out using the Mann-Whitney Rank Sum Test (Snedecor and Cochran, 1989).

Size at first maturity ( $L_{50}$ ) was also determined from the population of mature fish in each size group using a logistic curve fitted by a weighted non-linear least squares regression (SAS Institute Inc., 1988):

$$P_i = \frac{1}{1 + e^{-b(L_i - L_{50})}}$$

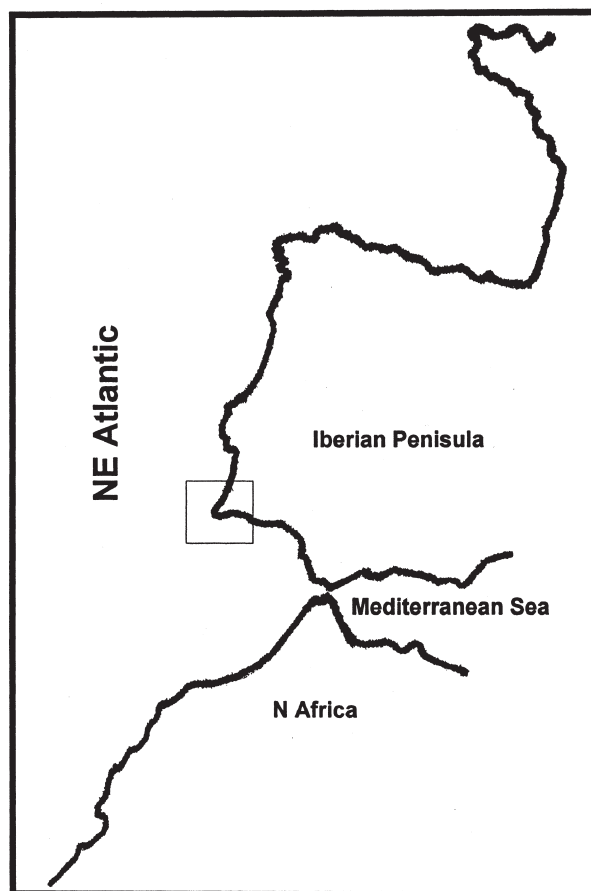


FIG. 1. – Fishing grounds for *Spondyliosoma cantharus* (small hook longline fleet) on the SW Coast of Portugal (Sagres-Costa Vicentina).

where  $P_i$  is the proportion of mature individuals of length class  $L_i$ ;  $b$  is a parameter determining the slope of the maturity curve and  $L_{50}$  is the size at which 50% of the fish are mature ( $P_i = 0.5$ ).

In order to avoid a misclassification between regressed and immature fish, only the fishes collected during the spawning season were considered for the analysis. Individuals were considered mature between macroscopic maturity stages IV to VI for males and IV to VII for females. Since the longlines used to catch the fish sampled are highly size selective, we also collected 32 smaller individuals (10.5 – 20.5 cm) with purse seines which are less size selective. Multivariate analysis (Hotelling's  $T^2$  test) was used to compare the parameter estimates for males and females (Bernard, 1981; Hanumara and Hoening, 1987).

Based on preliminary studies (Canário *et al.*, 1994), gonads at different maturity stages for both sexes and for hermaphrodites were fixed in either buffered Formalin (males) or San Felice solution (females) for histological studies. These gonads were embedded in paraffin wax, sectioned at 6-10  $\mu$ m and stained with Masson's Trichrome.

TABLE 1. – Macroscopic scale of maturation for females and males (adapted from Lagler, 1978) based on color, vascularization (+; ++; +++: low, medium and high degree of vascularization, respectively), proportion of the abdominal cavity occupied, presence of oocytes and signs of sperm releasing. (1) In stage III no oocytes are visible in the ovaries which are hyaline. (2) In stage IV oocytes are not visible in the ovaries which have a granular appearance. (3) In stage IV testes have already spermatozooids but do not release them. (4) Stage V coincides with the expelling of spermatozooids

| Stage          | Colour        | Vascularization | Abdominal Cav. (%) | Oocytes           | Maturation Stage Charact. |
|----------------|---------------|-----------------|--------------------|-------------------|---------------------------|
| <b>Females</b> |               |                 |                    |                   |                           |
| I              | uncoloured    | without         |                    | none              | Undetermined              |
| II             | rose          | onset           | <25%               | vestigial         | Resting Ovary             |
| III            | Yellow/Orange | onset           | 25%                | none (1)          | Onset development         |
| IV             | Yellow/Orange | +               | 50 to 75%          | none (2)          | Developing                |
| V              | Yellow/Orange | ++              | 100%               | present           | Pre-Spawning              |
| VI             | Yellow/Orange | +++             | 100%               | present - hyaline | Spawning                  |
| VII            | Reddish       | ++              | <100%              | vestigial         | Post-Spawning             |
| <b>Males</b>   |               |                 |                    |                   |                           |
| I              | uncoloured    | without         |                    | without           | Undetermined              |
| II             | grey/cream    | present         | <25%               | without           | Resting Testicule         |
| III            | grey/cream    | without         | 25%                | without           | Onset development         |
| IV             | white         | without         | 50 to 75%          | without (3)       | Developing                |
| V              | white         | without         | 100%               | with (4)          | Emission                  |
| VI             | white grey    | without         | <100%              | without           | Post-Emission             |

Following Shapiro (1984), sexual inversion length was estimated by aggregating the length frequency distribution where females and males overlap, and then calculating the median of the distribution.

The fecundity of 33 *S. cantharus* females sampled at the beginning of the spawning season was estimated gravimetrically. Mature ovaries (stage V, Table 1) were subsampled (0.01g) from the anterior, middle and posterior portions of each ovarian lobe. Optimas image analysis software (OPTIMAS, 1996) was used to count and to measure (diameter) the standing stock of advanced yolked oocytes. Under transmitted light these oocytes were completely opaque except for a perivitelline border. Kruskal-Wallis One Way ANOVA of ranks was used to test for spatial variations in oocyte density (oocytes/gram) and size (mean oocyte diameter) within the same lobe and between ovarian lobes. The absolute fecundity (Fa), which is the number of mature oocytes spawned by a female in a single spawning (Bagenal, 1973) was estimated:  $Fa = GW \times D$ , where GW is the weight of the ovary and D is the density of mature oocytes (number of oocytes per g of ovarian tissue). Relative fecundity (Fr) was estimated as the number of mature oocytes per gram of female somatic weight (SW = total weight – gonad weight) (Bagenal, 1973):  $Fr = Fa/SW$ . The relationships between the absolute fecundity (Fa) and somatic weight (SW) and total length (TL) were evaluated with linear, logarithmic, exponential, power and polynomial regressions.

Additional information concerning reproductive cycles and strategies, specially hermaphroditism,

was reviewed for a more complete understanding of the reproductive biology of the black sea bream.

## RESULTS

### Spawning season

Overall, the mean GSI was 1.2%, ranging from 0.0% to 12.6% (♂ 0.0-2.9%; ♀ 0.1-12.6%). Monthly mean values ranged from 0.1 to 3.6% (n=386), varying between 0.1 and 1.1% (n=81) for males and 0.3-5.7% (n=185) for females. *S. cantharus* is a winter-spring spawner, spawning from February to April, with a single peak in March for both years (1993/94) (Fig. 2). The resting period effectively extends from July to December. The maturation process is slower for males, giving GSI peaks one month after females, especially in 1994. The Febru-

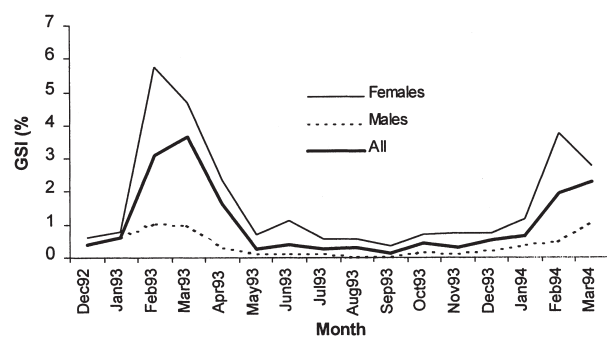


Fig. 2. – Annual cycle of gonad-somatic index (GSI) (males, females and all genders combined: both sexes plus hermaphrodites and individuals of indeterminate sex) for *Spondyliosoma cantharus*. Total sample size = 368 individuals

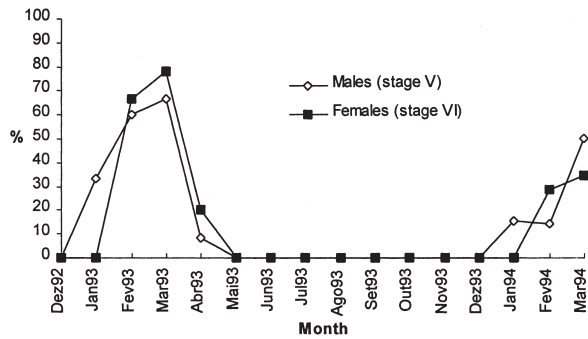


FIG. 3. – Evolution of advanced spawning stages percentage for each sex (spawning females - stage VI and males in emission - stage V) for *Spondyliosoma cantharus*. Total sample size = 266 individuals

ary peak for the females is one month before the general GSI peak. GSI values for females were much higher than those of males (Fig. 2).

Outside the spawning season males and females were practically indistinguishable. However, during the breeding season almost 50% of the males showed a darker coloration and 90% had a characteristic blue-violet spot between the eyes. All individuals exhibiting this coloration pattern were males, corroborating in this way, the behavioural observations made in aquariums by Wilson (1958).

Macroscopic analysis of the gonads showed that both females and males exhibited the same patterns in terms of the maturity stages (Fig. 3), with the same highest percentage of spawning individuals (Stages V and VI for males and females, respectively) in March (1993/4). However, males started their spawning period one month before females (January).

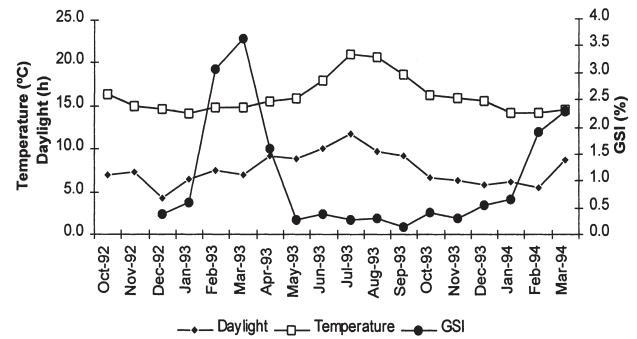


FIG. 4. – Monthly variation of mean GSI values for *Spondyliosoma cantharus*, sea surface temperature (Praia da Rocha) and daylight hours (Cabo de Santa Maria) from October 1992 to March 1994 (environmental data supplied by the Instituto de Meteorologia)

Females in post-spawning condition (stage VI) were found from the end of the spawning period until August; while females in the earlier stage V were found in June, suggesting a longer spawning season than that based on the GSI.

Results of the histological analysis were generally in agreement with the macroscopic analysis of the gonads. However, due to the relatively small sample size of the histological study, it was not possible to make a statistically valid comparison between histological and macroscopic stages.

No significant correlations were found between mean GSI values and mean daylight hours and sea surface temperatures ( $r = -0.14$ ,  $P > 0.05$  and  $r = -0.47$ ,  $P > 0.05$  respectively) (Fig. 4). Nevertheless, the spawning of the black sea bream took place during the period of increasing SST and daylight hours. During the 1992-93 spawning period the mean daylight hours and SST were  $7.9 \pm 1.2$  hours (s.d.) and

TABLE 2. – Monthly number of individuals (n) sampled by sex (males, females, hermaphrodites with predominant ovary (Fm), hermaphrodites with predominant testis (Mf) and unsexed individuals) and size range by sample for *Spondyliosoma cantharus*

| Month       | Female | Male | Fm | Mf | Unsexed | Total | Size range |
|-------------|--------|------|----|----|---------|-------|------------|
| Dec92       | 3      | 0    | 0  | 0  | 0       | 3     | 22.5-29.5  |
| Jan93       | 3      | 3    | 0  | 0  | 0       | 6     | 21.5-26.5  |
| Feb93       | 6      | 5    | 0  | 0  | 0       | 11    | 21.0-29.0  |
| Mar93       | 22     | 6    | 0  | 0  | 0       | 28    | 21.0-33.0  |
| Apr93       | 33     | 12   | 0  | 0  | 9       | 54    | 19.0-27.7  |
| May93       | 5      | 3    | 0  | 0  | 0       | 8     | 22.0-30.5  |
| Jun93       | 3      | 4    | 0  | 0  | 0       | 7     | 23.0-32.5  |
| Jul93       | 5      | 1    | 0  | 0  | 0       | 6     | 23.5-29.0  |
| Aug93       | 10     | 5    | 1  | 1  | 0       | 17    | 22.5-33.5  |
| Sep93       | 6      | 3    | 1  | 4  | 0       | 14    | 22.0-31.0  |
| Oct93       | 15     | 2    | 0  | 0  | 0       | 17    | 20.5-28.0  |
| Nov93       | 5      | 6    | 3  | 1  | 0       | 15    | 21.0-30.0  |
| Dec93       | 20     | 2    | 1  | 0  | 0       | 23    | 20.0-29.9  |
| Jan94       | 12     | 13   | 0  | 2  | 0       | 27    | 20.8-35.5  |
| Feb94       | 14     | 14   | 0  | 0  | 0       | 28    | 19.5-27.5  |
| Mar94       | 23     | 2    | 0  | 0  | 0       | 25    | 20.0-28.5  |
| Grand Total | 185    | 81   | 6  | 8  | 9       | 289   | 19.0-35.5  |

15.0±0.3 (s.d.) °C respectively (Fig. 4). The SST ranges for both spawning seasons were 14.8-15.4°C and 14.1-14.4°C (only February and March 1994) respectively.

### Sex ratio

Throughout the study the sex ratio was dominated by females (annual average ratio M/F = 0.57±0.44; Table 2), with the exception of the period prior to the spawning season (Kolmogorov-Smirnov test,  $k_s = 0.375$ ,  $P = 0.215$ ). The range of lengths sampled was from 19.5 to 35.5 cm, with the lower limit determined by the selectivity of the fishing gear (Erzini *et al.*, 1996). There were no males in the smallest length classes (19.5-20.5 cm) (Fig. 5). The smallest males were in the 21.5 cm class which also included hermaphrodites (Fig. 5), and there were almost no females in the largest length classes. Average length at capture was different for the two sexes (M: 26.7±2.7 and F: 23.3±2.0 cm; Mann-Whitney Rank Sum Test,  $T = 16324.5$ ,  $P < 0.001$ ).

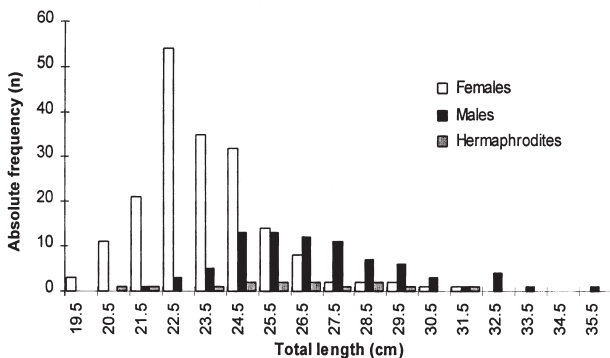


FIG. 5. – Total length frequency distributions of males, females and hermaphrodites for *Spondyliosoma cantharus*. Total sample size = 280 individuals

### Length at first maturity

The lengths at 50% sexual maturity were significantly different (Hotelling's  $T^2$ ,  $df = 6$ ,  $T^2 = 19.89$ ,  $P < 0.05$ ), with 19.98 cm ( $\pm 0.27$  std. error) and 22.41 cm ( $\pm 0.60$  std. error) for females and males, respectively. Length at first maturity calculated for both sexes, hermaphrodites and indeterminate sex individuals combined was 20.10 cm ( $\pm 0.78$  std. error and 95% confidence interval of 18.49-21.71) (Fig. 6). This size at 50% maturity corresponded to 2-3 years of age (Gonçalves, unpublished data).

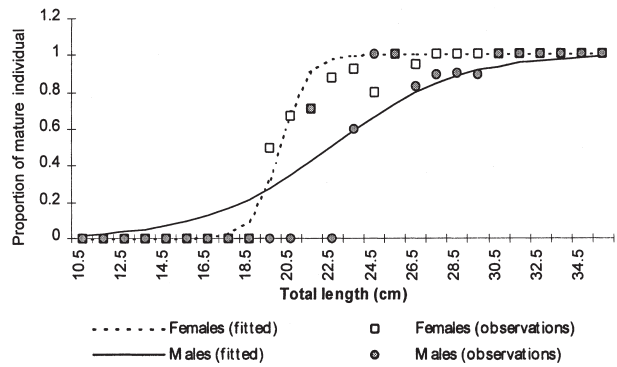


FIG. 6. – Proportion of mature individuals by total length for males and females (“observations”) and maturity ogive (logistic curve - “fitted”) fitted by weighted non-linear least-squares regression

### Hermaphroditism

Within the few hermaphrodites found ( $n = 14$ , 5.0%), one of the sexes was always predominant, and the average total length was also higher for the individuals with a major male fraction (Mf: 27.9±1.8 cm, Fm: 23.1±2.1 cm). The average total length of the hermaphrodites as a whole (25.9±3.1 cm) was intermediate between the two sexes (F: 23.3±2.0 cm and M: 26.7±2.7 cm). Sexual inversion occurs at approximately 24.5 cm, which is the distribution median of 352 individuals from 21.5-31.5 cm. The hermaphrodites appeared in major concentration in the autumn months, especially in September and in November, which is the resting period. Evidence of regression of female sex cells was noted in some Mf gonads.

### Fecundity

Density of oocytes did not vary significantly among positions (anterior, medial and posterior) within the same ovarian lobe or between lobes (Kruskal-Wallis One Way ANOVA on Ranks,  $H = 0.557$ ,  $df = 5$ ,  $P = 0.990$ ). The values of the mean diameter also did not vary significantly between positions within ovarian lobes (Kruskal-Wallis One Way ANOVA on Ranks,  $H = 0.066$ ,  $df = 2$ ,  $P = 0.967$ ). Thus, samples for absolute fecundity were combined from the different positions and ovarian lobes. From a sample of 30 oocytes per ovary ( $n = 990$ ), only 18 (1.8%) presented signs of pre-ovulatory atresia. The mean diameter of oocytes in advanced vitellogenesis was 654±4.9µm (408-885 µm;  $n = 460$ ). The relations between the absolute fecundity (Fa) and somatic weight (SW) and total length (TL) were best described by power equations:

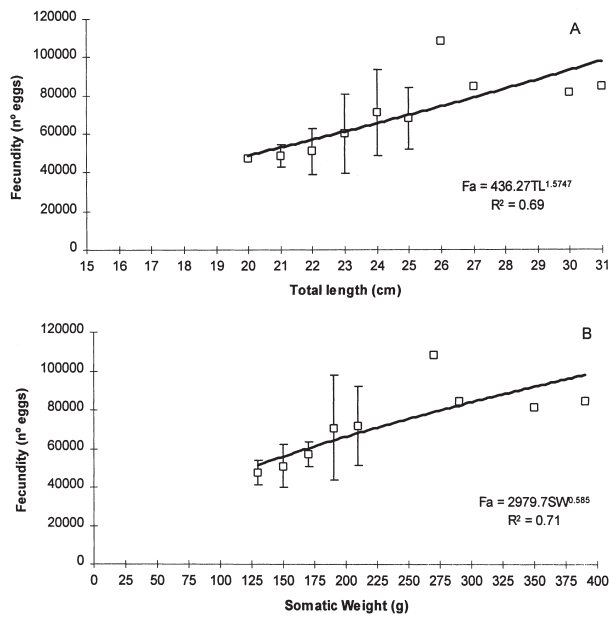


FIG. 7. – Relation between mean absolute fecundity ( $\pm$  s.d.) and A) total length (TL, cm), B) somatic weight (SW, g) for *Spondyliosoma cantharus*

$Fa = 436.27TL^{1.575}$  ( $r^2 = 0.69$ ) and  $Fa = 2979.7SW^{0.585}$  ( $r^2 = 0.71$ ), respectively (Fig. 7). Absolute fecundity estimates ranged from 37506 (22.0 cm; 137.3g) to 112074 (24.5 cm; 216.8g) eggs. Based on somatic body weight the number of eggs/g ranged from 217 to 549, with a mean value of  $346 \pm 80$  (s.d.) eggs. The mean value for absolute fecundity was  $61396 \pm 19594$  for a mean total length  $23.3 \pm 2.4$  cm (20.9–31.5 cm), a mean somatic weight of  $182.2 \pm 62.2$  g (120.1–388.4g) and a mean gonad weight of  $8.5 \pm 4.7$  g (3.3–22.0g).

## DISCUSSION

Analysis of the GSI together with maturity stage data for males and females showed that the spawning season extends from February to April, with a peak in March. These data are largely in agreement

with Bauchot and Hureau (1986) for the Atlantic (Table 3) and also Ojeda (1983 in Balguerías *et al.*, 1993) and Florido (1986 in Balguerías *et al.*, 1993) who reported a spawning season from January to April, and in March, respectively, in the Canary Islands. Other authors from the Mediterranean recorded a shorter and later spawning season. In the Atlantic Coast of France the spawning season was even later (Table 3).

Mean monthly values of GSI were not significantly correlated with SST or with the number of daylight hours, suggesting that other factors may be more important for sexual maturity. The fact that this species has benthic eggs implies that biotic factors such as predation and parental care may be more relevant for reproduction than environmental factors such as currents (Potts, 1984). Along the Portuguese Southwest coast, summer upwelling beginning in June and ending in September contributes to greater productivity but also to high rates of egg and larval predation (Afonso, 1995). However, the role of upwelling in the reproductive cycles of sparid fishes is still largely unknown.

In this study spawning took place over a temperature range from 14.1 to 15.4°C, although *S. cantharus* has been known to spawn in captivity at temperatures ranging from 12 to 14°C (Wilson, 1958).

Concerning the sex ratio, as in other studies by Lozano *et al.* (1990) and Balguerías *et al.* (1993), females were predominant throughout the sampling period, especially for the smaller size classes, while males were relatively more abundant in the larger size classes. This was particularly true during the warmer seasons and may be a consequence of sequential hermaphroditism. In fact, Perodou and Nedelec (1980) observed a seasonal and age differential distribution, in which juveniles remained in coastal waters until 3 years of age, after which they migrated to deeper waters (50–100m) in the winter and returned to inshore waters in the summer. Knowing that the female percentage decreased grad-

TABLE 3. – Spawning seasons of *Spondyliosoma cantharus* reported by other authors

| Authors                         | Region                        | Spawning Season |
|---------------------------------|-------------------------------|-----------------|
| Perodou and Nedelec (1980)      | English Channel               | May-June        |
| Soletchnik (1983)               | English Channel               | April-May       |
| Quéro (1984)                    | Gulf of Biscay                | May-June        |
| Bauchot and Hureau (1986)       | NE Atlantic and Mediterranean | February-May    |
| Riedl (1986)                    | Mediterranean                 | April-May       |
| Fischer <i>et al.</i> (1987)    | Mediterranean                 | March-May       |
| Balguerías <i>et al.</i> (1993) | Sahara Bank                   | May-August      |
| Present study                   | SW Coast of Portugal          | February-April  |

ually with increasing size (and consequently with age), that the fishing grounds of small hook longline fisheries in the Portuguese South West coast are located at depths between 30 and 80 m (30–40 m in the summer), and given the relatively small mean size of the fish caught by this gear, the observed sex ratios are not unexpected. Besides, as discussed later, the mating behaviour of this species, which is characterised by demersal eggs and parental (male) care, makes it difficult to capture males with this gear, especially during the spawning season.

Average length at capture was different for both sexes, with males having a larger mean size than females, which is in agreement with the results of other authors (Perodou and Nedelec, 1980; Soletchnik, 1983; Lozano *et al.*, 1990 and Balguerías *et al.*, 1993), and once more is probably a consequence of sequential hermaphroditism. As Buxton and Garratt (1990) stated for South African protogynous sparids, the sex reversing individuals have a size intermediate between the two sexes.

The different sizes of first maturation presented by males and females reported by Lozano *et al.* (1990) (19.5 cm for both sexes; 18.7 cm for females and 27.3 cm for males) suggest different conditions in terms of productivity, fishing intensity, temperature and consequently in the sexual inversion rate, between the south of Portugal and the Canary Islands. Other authors, reported 20 cm (2 years) (Perodou and Nedelec, 1980), 23–24 cm (3 years) (Soletchnik, 1983) and 14–15.2 cm (Fork Length) (Balguerías *et al.*, 1993).

The current 23 cm (TL) minimum legal size ruled in the Portuguese fishery is higher than our estimate of size at 50% maturity. The length composition of hook longline samples shows that 12.7% (Gonçalves, unpublished data) or 28.8% as suggested by Erzini *et al.* (1995, 1997) of the fish caught in the fishery are smaller than our estimate of length at 50% maturity. Our results suggest that more than a change in the legal minimum fish length, a reinforcement of the actual legislation is required for a better conservation of this species.

Features such as transitional individuals, testes with rudiments of the former ovary and biased sex size-frequency distributions, indicate a reproductive strategy based on protogynous hermaphroditism (Sandovy and Shapiro, 1987), as first reported by D'Ancona (1949). Individuals mature first as females and then after an intermediate period undergo a sexual inversion, turning into males. Nevertheless, due to the occurrence of small males that apparently did not

change sex, the hypothesis of the existence of a reduced number of primary males can not be excluded (Alekseev, 1982; Balguerías *et al.*, 1993).

As reported by Soletchnik (1983), for fish from the English Channel, sexual inversion occurs mainly in Autumn. Length at sexual inversion was 24.5 cm, which is similar to what Balguerías *et al.* (1993) reported for the Sahara Bank (23.34 cm, Fork Length), but very different from the 35 cm (TL) provisionally estimated by Perodou and Nedelec (1980) for the Northern part of the Gulf of Biscay.

There are advantages for larger males with regards to the reproductive behaviour of this species. The males dig a hole in the sand where the females deposit their eggs and protect them until the time of hatching (Wilson, 1958). The larger males have a higher probability of success in defending their territory and therefore of achieving reproductive success. In this species a protogynous reproductive strategy confers an ecological advantage as a consequence of the fact that reproductive success seems to be size related.

The demersal eggs and nesting behaviour of *S. cantharus* are unusual since sparid eggs are usually pelagic. *S. emarginatum*, a southern African endemic sparid, is another exception, (Beckley, 1989), although this is probably a case of a gonochoristic species (Penrith, 1972). Nevertheless there are more sparid species with the same hermaphroditic reproduction strategy, such as *Pagellus erythrinus* (D'Ancona, 1949; Larrañeta, 1964; Girardin and Quignard, 1985) and *Pagrus pagrus* (Manooch III and Hassler, 1978; Alekseev, 1982, 1983).

In terms of stock assessment, the fact that males are dominant in the upper length classes and are the nest guards, could mean that in case of over-fishing there would be a deficit in the spawning stock, unless *S. cantharus* is able to increase its sexual inversion rate and temporarily compensate. According to the studies of Thompson and Munroe (1978), this can occur with *Epinephelus guttatus* (Serranidae), where they suggested that the proportion of males increased with the exploitation of the population. Overexploitation of smaller individuals, consisting mostly of females, is likely to have a negative impact on the stock through a reduction in the reproductive potential and could also result in a replacement of functional protogyny by juvenile protogyny (Alekseev, 1983). This author studied different population structures in protogynic porgies (*Pagrus* spp.) and found that there could be a decrease in the selective value of functional protog-

ny with the reduction in life span associated with increased exploitation.

The possibility of batch spawning episodes in the case of *S. cantharus* can not be excluded because of the existence during the entire spawning period of oocytes in different stages of development. Since it was not possible to confirm determinate fecundity (Hunter *et al.*, 1992) in this species, the estimates should be considered minimum potential annual values.

The absolute fecundity of the black bream increased in a non-linear manner with total length and somatic weight of females. However, the increase was not continuous, with an apparent decrease in fecundity for the largest individuals. No differences in density or size distributions of the eggs were found between the two lobes and within each lobe of the gonads. Thus, for future studies, samples can be taken from any part of the gonads.

The other fecundity data available for *S. cantharus* are those of Balguerías *et al.* (1993) for Sahara bank (eastern Atlantic) and Dulčić *et al.* (1998) for Adriatic sea. The first authors used oocyte diameter ranging from 0.55 to 1.7 mm (average 0.906 mm) and reported considerably smaller values for relative fecundity (206 compared to 346 oocytes/g), with a similar range (36,926-143,900 oocytes) and mean values (65,659 oocytes) for absolute fecundity. The latter authors found that absolute fecundity ranged from 31,670 to 554,070 eggs/female, for an oocyte diameter range from 0.5 to 0.8 mm. The differences between these studies might be due to the differing methodologies used; namely in terms of the size range of the fish sampled, the oocyte size threshold and the oocyte size range, rather than classic causes (nutritional, genetic and environmental). The relatively low fecundity of the black bream may be related to the reproductive behaviour; namely parental care, with associated potential increases in fertilisation and hatching rates. This protogynous strategy could perhaps explain why the reproductive potential of individual *S. cantharus* is less than that of other species of the same family, such as *Pagellus bogaraveo* (Krug, 1990) or *Diplodus vulgaris* (Gonçalves and Erzini, 2000) which have the opposite reproductive strategy.

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