Reproductive biology and recruitment of the white sea bream in the Azores

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The life history of the white sea bream *Diplodus sargus* in the Azores showed a pattern consistent with digynic hermaphroditism achieving sexual maturity during the second year of life, at $16 \cdot 7$ cm L_T. Spawning occurred from March to June at temperatures between 15 and $17° C$ and the onset and duration of spawning season in the sea bream appeared to be influenced by sea water temperatures. As latitude decreased, both in the northern and southern hemispheres, the spawning season of *D. sargus* populations started earlier and extended longer, highlighting the potential importance of temperature to the onset and duration of reproduction in this species. Settlement took place from late May to July, and settlers remained in the nursery area for *c.* $2 \cdot 5$ months. Emigration from the nursery area to join shoals of juveniles occurred from late July to September. © 2003 The Fisheries Society of the British Isles

Key words: *Diplodus sargus*; insular populations; maturity; settlement; sex ratio; spawning.

INTRODUCTION

The reproduction and recruitment of shore fishes have been well studied for populations from the north-eastern Atlantic and the Mediterranean (Gibson, 1969; Faria *et al.*, 1996; Vigliola *et al.*, 1998; Gonçalves & Erzini, 2000). In contrast, little work has been done on the populations inhabiting the shore habitats of the north Atlantic oceanic islands. Patterns in the reproduction and recruitment of fishes can be highly influenced by environmental conditions and habitat characteristics, including food, predators, temperature, salinity, oxygen, habitat structure, topography and hydrodynamics (Gibson, 1994). Because such conditions can vary substantially between continental and oceanic shore habitats comparative studies using continental and insular populations can elucidate plasticity in reproductive traits due to differing environmental pressures. Additionally, hypotheses concerning the ecological functioning and evolution of life-history strategies can be tested.

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Buxton & Garratt (1990) reviewed the reproductive strategies of the Sparidae and suggested that they are either sequential hermaphrodites (changing from one functional sex to the other) or rudimentary hermaphrodites (immatures with intersexual gonads but either male or female mature adults). Protandry (Micale *et al.*, 1987; Abou-Seedo *et al.*, 1990; Micale & Perdichizzi, 1994; Martínez-Pastor & Villegas-Cuadros, 1996) and rudimentary hermaphroditism (Joubert, 1981) has been reported in the white sea bream *Diplodus sargus* L. Coetzee (1986) and Mann & Buxton (1998), however, found that the white sea bream could also be digynic, where both males and females mature from a non-functional intersexual phase, with some males retaining the ability of changing sex into secondary females. Furthermore, Mann & Buxton (1998) pointed out the lack of clarity in the terminology applied in several studies and concluded that digyny is probably a common reproductive style in *D. sargus*. Such differences found in continental populations of *D. sargus* highlight its potential for reproductive plasticity over its extensive geographical distribution and the importance of studying insular populations.

In this study the reproductive biology of *D. sargus* in the Azores, an insular population, was investigated and compared with information available from other regions.

MATERIALS AND METHODS

A total of 1126 individuals were obtained between August 1997 and July 1999 in the Azores archipelago. Fish were caught by spear fishing, hook and line and SCUBA hand netting. Samples were collected on a monthly basis in the island of Faial and once each summer in 1997, 1998 and 1999 at the islands of Corvo and Santa Maria (Fig. 1). On each sampling occasion 20 individuals from each of three size categories (small, <15 cm total length, L_T; medium, 15–30 cm L_T; large, >30 cm L_T) were retained. Juveniles were obtained from monthly beach-seining at Porto Pim Bay, Faial Island. The seine was
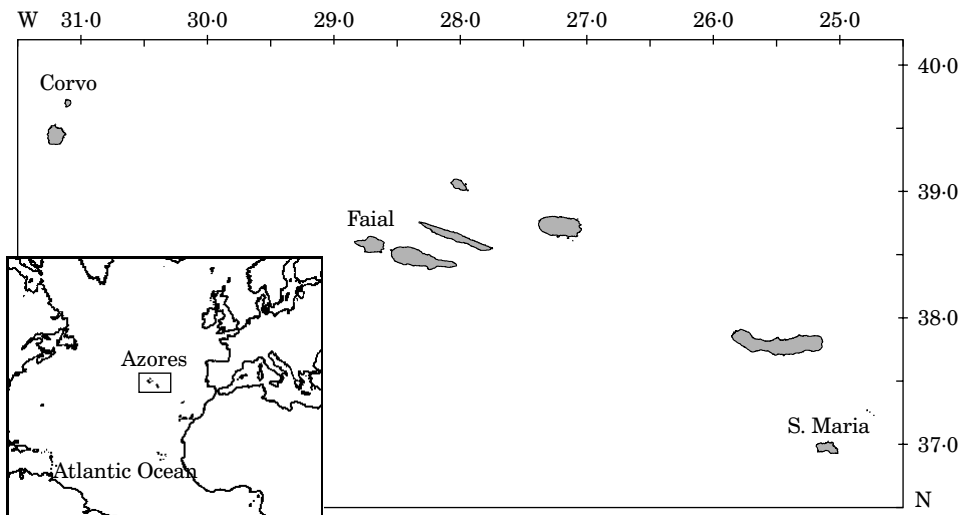

FIG. 1. Location of the Azores archipelago, Portugal, showing the sampled islands of Faial, Corvo and Santa Maria.

20 m long (32 mm stretch mesh in the wings reducing through 15 mm to 8 mm in the centre). Effective fishing area (291 m^2 per haul) was estimated by using the method of Kubecka & Bohm (1991). The seine was fished at low tide at night with a new moon, to reduce the variability in catches due to tidal, daily and lunar patterns in the community structure (Nash & Santos, 1998) and catchability of this species.

In the laboratory, L_T (cm) and eviscerated mass (M_E, g) were recorded. Gonads were removed and weighed (M_G). Each individual was sexed and gonads were macroscopically staged as either immature (stage 0), resting (stage 1), developing (stage 2), pre-spawning (stage 3), spawning (stage 4) or spent (stage 5) (adapted from Buxton, 1990). Although many fish across the size range studied showed evidence of hermaphroditism, fish were sexed macroscopically according to the dominant sexual tissue in the gonad. Individuals were classed as intersexes when male and female parts of the gonads occurred in equal proportions. It was not possible to macroscopically identify the sex of individuals <12 cm L_T. Sagittal otoliths were removed from 796 individuals over the whole size range and standard techniques used for ageing fish and subsequently to estimate age at first maturity. The seasonality of zone deposition was determined by marginal increment analysis.

Sex ratio, expressed as a male : female ratio, was analysed over 1 cm L_T classes and by season. Months were grouped based on the maturity cycle: developing, November to February; pre-spawning and spawning, March to June; recovering and resting, July to October. Deviations from the 1:1 null hypothesis were statistically tested by χ^2. Differences in mean lengths of females and males were tested by single-factor ANOVA (Zar, 1999).

Total length (L_{T50}; $n = 1120$) and age at first maturity (A_{50}; $n = 753$) were estimated for the pooled sexes by fitting the relative frequency of all mature individuals (stages 1–5) over 1 cm L_T classes and by age to logistic curves, using the Levenberg–Marquardt algorithm (Marquardt, 1963) for solving the nonlinear least-squares regression: $P_X = [1 + e^{-a(X-b)}]^{-1}$, where P_X is the proportion of mature fish at L_T or age X; a and b are estimated parameters, where a is the slope of the curve and b corresponds to a proportion of 0·5 mature fish.

Spawning period was determined by analysing the monthly variation in gonadal maturity stages, as well as the mean gonado-somatic index (I_G). Individual I_G were calculated only for individuals with lengths >L_{T50}, using M_E. Condition status was determined on a monthly basis from Fulton's condition factor (K) where $K = 1000 M_E L_T^{-3}$. Correlation between I_G and K was tested using the Spearman rank correlation coefficient (r_s) (Zar, 1999).

Water temperature was measured at 30 min intervals at each of the three islands using underwater dataloggers (StowAway®, TidbiT®; Bourne, U.S.A.), from August 1997 until the end of the study. Stations were located at 25 m depth on exposed rocky shores, as these conditions were considered to approximate to the habitat and average depth distribution of the species in the region, especially mature individuals. Water temperatures from each month were averaged and the mean temperatures for each month over the 2 years were averaged to give an indication of the annual thermal regime in the area.

RESULTS

REPRODUCTIVE BIOLOGY

The white sea bream caught in this study ranged from 1·7 to 41·1 cm L_T. Males and females had similar length–frequency distributions, with no clear separation in modal size between sexes (Fig. 2). Females dominated size classes >20 cm L_T (Fig. 3), however, and males showed an abrupt decrease in abundance between 21 and 23 cm L_T. Average L_T of males was significantly smaller than that of females (24·5 *v.* 27·1 cm L_T; ANOVA, $n = 677$; $P < 0·001$). Only 10 intersex gonads were observed in fish ranging in size from 12·9 to 22·9 cm L_T.
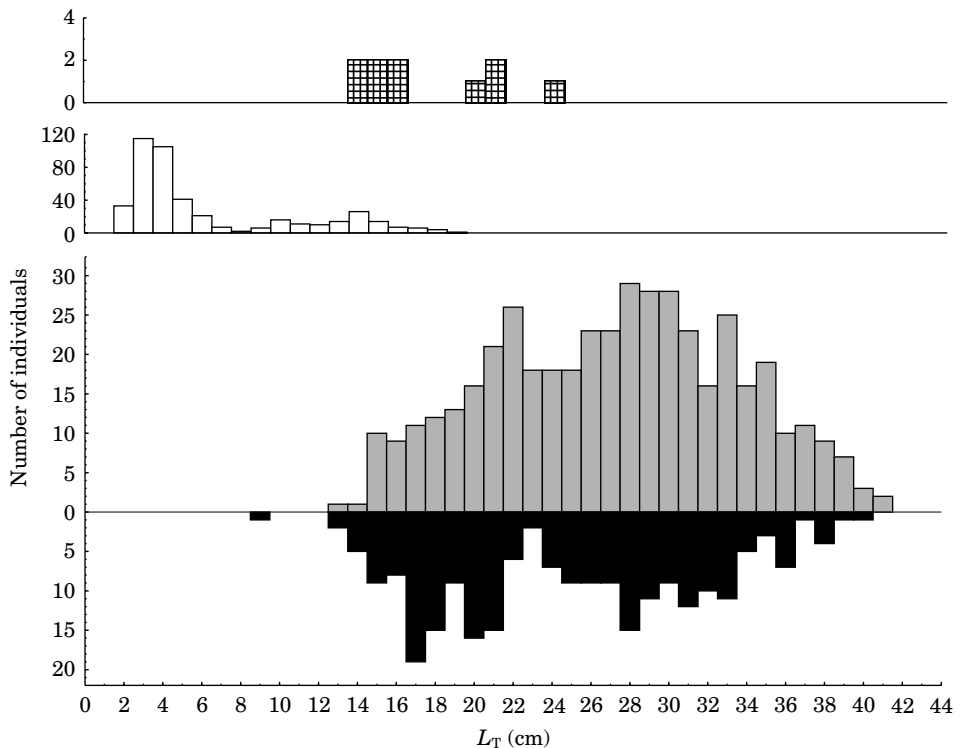
FIG. 2. Length–frequency distribution of female (▦), male (■), unsexed (□) and intersexed (⊞) *Diplodus sargus* for the period 1997–1999.

The overall sex ratio (Table I) was 1 male to 1·93 females, diverging significantly from 1 : 1 (χ^2, $n = 677$; $P < 0.001$), and there was 1 male for 0·04 intersex fish. Sex ratio varied with season from 1 : 1·56 (March to June) to 1 : 2·84 (November to February). These values, however, could have been influenced by the different mean sizes of the fish sampled during each period. The highest and the lowest proportion of females corresponded to the periods of high and low mean sizes of the fish sampled, respectively.

The length and age at maturity (Fig. 4) were estimated for the pooled sexes. L_{T50} was estimated as 16·73 cm (s.d. = 0·18) while A_{50} was estimated as 2·12 years (s.d. = 0·04).

The proportion of mature *D. sargus* at each macroscopic maturity stage varied with season (Table II). Pre-spawning individuals were first observed in January (0·22), when the mean water temperature decreased to *c.* 16° C, and increased in proportion during February (0·89). Spawning individuals began to appear in March, when mean water temperature started to warm from its minimum (*c.* 15° C), and the proportion of pre-spawning individuals decreased. The spawning period extended throughout the spring until June, ceasing when mean water temperature increased to >17° C. Post-spawning individuals were observed from March to September. Individuals with resting and developing gonads were observed from the month after the end of the spawning season until January, but developing gonads were also observed in February and March.
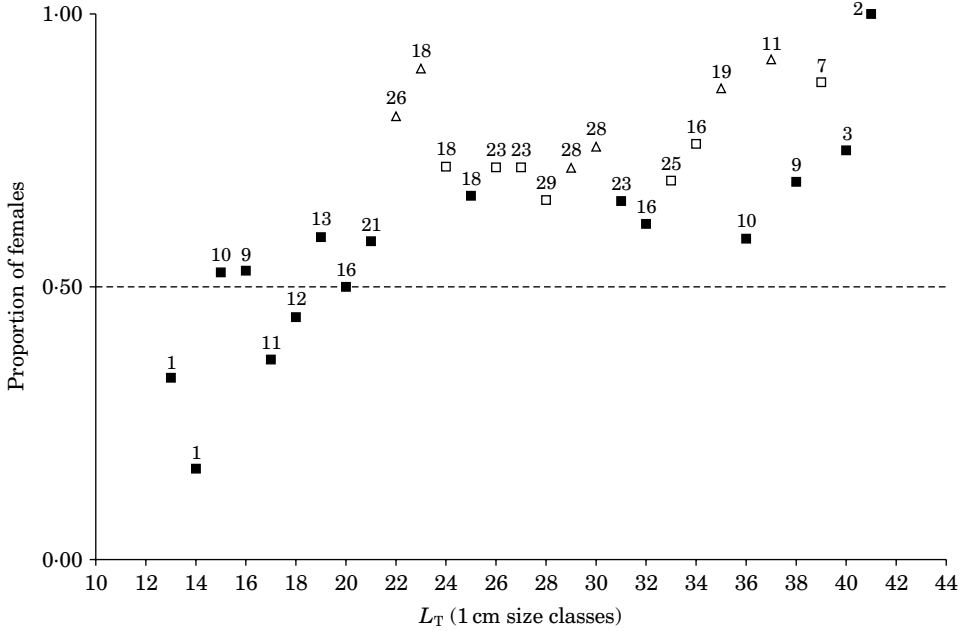
FIG. 3. Proportion of *Diplodus sargus* females, by length class for the period 1997–1999. Significance of χ^2 test: ($\triangle$) $P < 0.01$; ($\square$) $P < 0.05$; ($\blacksquare$) NS. Numbers of females are also given.

The monthly I_G (Fig. 5) was highly associated with the seasonality of the maturity stages assigned macroscopically and water temperature. An increase in the I_G was observed from January to February as mean water temperature decreased to *c*. 17° C, and pre-spawning individuals appeared. The I_G peaked in March at water temperatures of *c*. 15° C, corresponding to the first observation of spawning individuals. A decrease in the I_G from March to June, coincided with the spawning season. During this period water temperature varied from 15·5 to 17·7° C. When water temperature increased to *c*. 18° C, the I_G stopped decreasing and stabilized at a low value. From July to December, the I_G was low and corresponded to the resting and early developing period. The relationship between spawning activity and mean water temperatures indicates optimal

TABLE I. Total and seasonal sex ratio (M : F) of *Diplodus sargus* from the Azores over the period 1997–1999. χ^2 and *P*-values for testing the 1 : 1 hypothesis, and mean total length seasonally and for the total period are also given

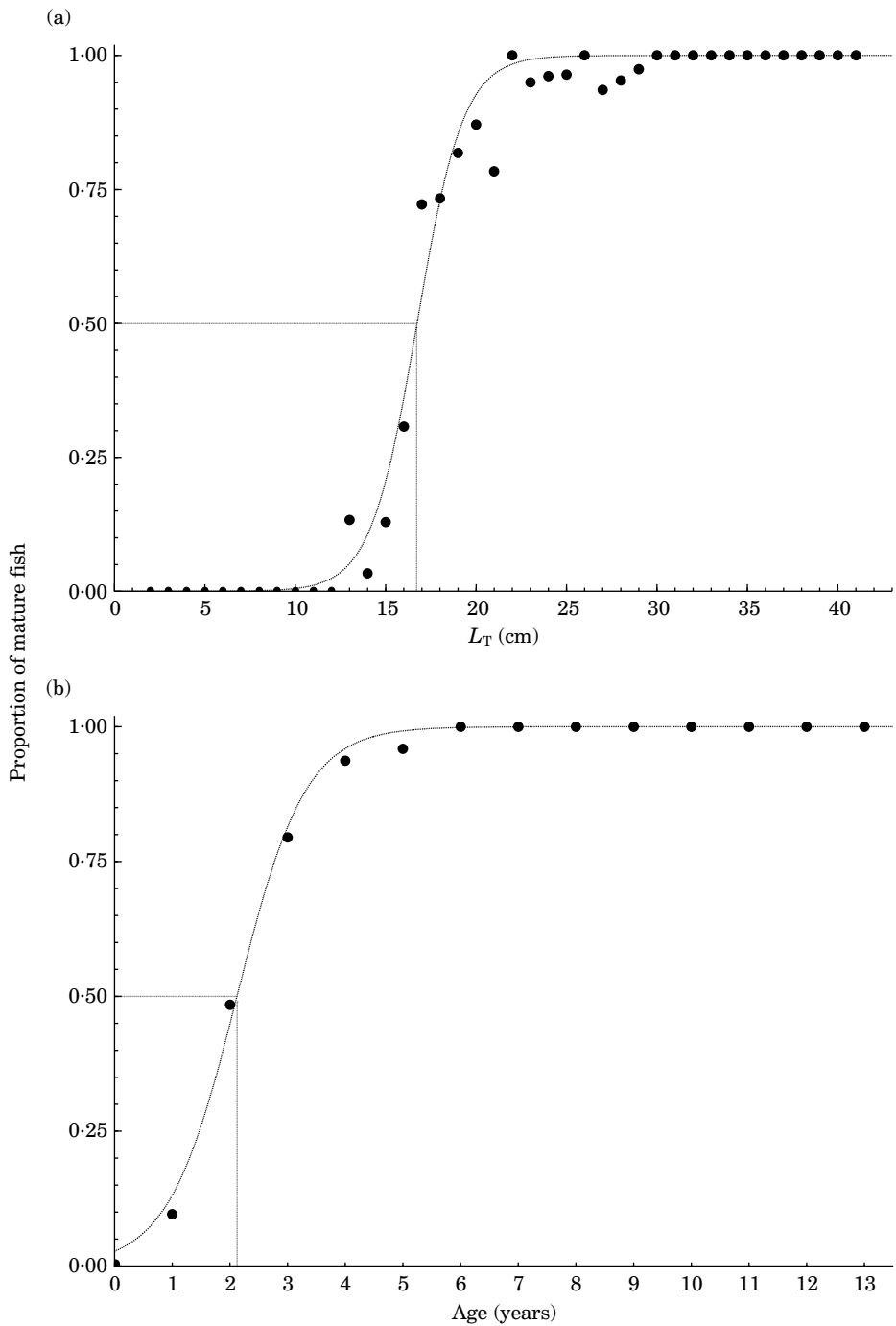| Season	Maturity stage	M : F	χ^2	P	n	Mean L_T (cm)
November–February	Developing	1 : 2·84	39·82	<0·001	173	22·6
March–June	Pre-spawning and spawning	1 : 1·56	12·54	<0·001	259	15·5
July–October	Recovering and resting	1 : 1·88	22·96	<0·001	245	19·4
Total period		1 : 1·93	68·26	<0·001	677	18·2

(a)

(b)

FIG. 4. Maturity ogives of (a) total length and (b) age at first maturity of *Diplodus sargus* for the period 1997–1999. $L_{T50} = 16·73 \pm 0·18$ cm; $y = [1 + e^{-0·780(x - 16·733)}]^{-1}$, $r = 0·994$, $n = 1120$. $A_{50} = 2·12 \pm 0·04$ years; $y = [1 + e^{-1·684(x - 2·122)}]^{-1}$, $r = 0·998$, $n = 753$.

TABLE II. Monthly proportion of maturity stages in *Diplodus sargus* and mean water temperature (°C) for the Azores archipelago over the period 1997–1999. Maturity stages are: 1, resting; 2, developing; 3, pre-spawning; 4, spawning; 5, spent

| Month	Maturity stages						Temperature (°C)	
	1	2	3	4	5	*n*	Mean	Range
January	0·22	0·56	0·22			9	16·5	14·3–18·5
February		0·11	0·89			19	15·7	14·0–17·4
March		0·11	0·71	0·17	0·01	128	15·5	14·0–17·6
April			0·14	0·60	0·26	43	15·9	13·9–19·3
May			0·43	0·52	0·06	55	16·7	14·0–19·3
June			0·21	0·71	0·07	15	17·7	14·0–20·8
July	0·54	0·26			0·20	50	18·9	14·8–23·1
August	0·22	0·60	0·02		0·15	86	21·1	14·6–24·5
September	0·43	0·45			0·12	76	21·5	15·1–24·2
October	0·33	0·67				3	20·7	15·1–23·3
November	0·26	0·72	0·01			69	19·1	15·3–22·3
December	0·13	0·87				54	17·7	15·0–20·5
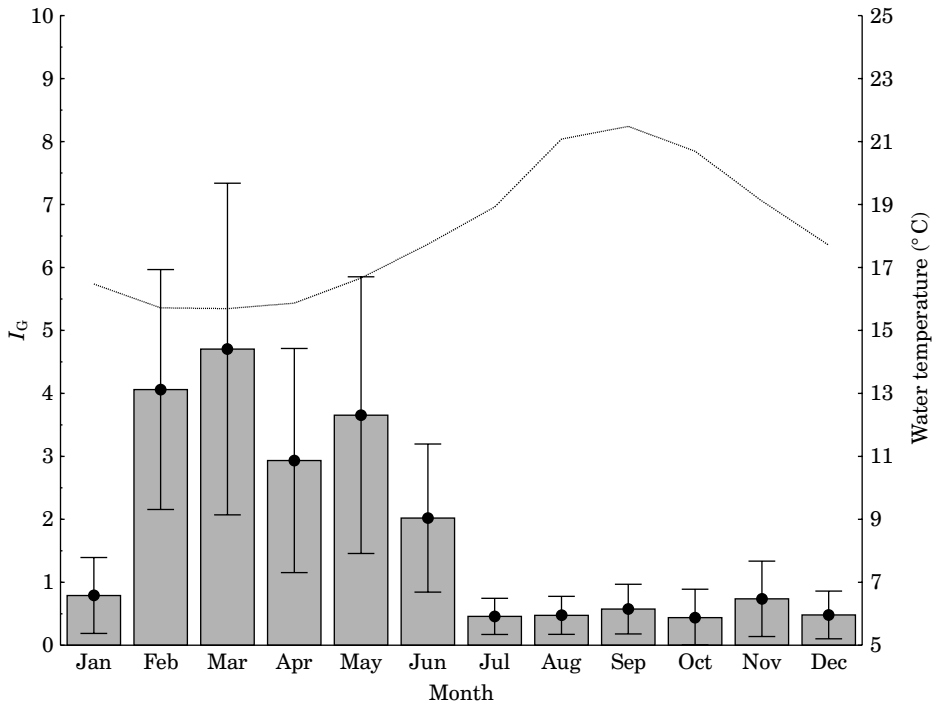
FIG. 5. Monthly mean ± S.D. gonado-somatic index (▨) for mature *Diplodus sargus* (sexes pooled). Mean monthly sea temperature at 25 m depth (·········) is also given.

spawning temperatures range between 15 and 17° C. Monthly mean I_G did not vary between males and females during the pre-spawning and spawning periods (January to June), indicating that ovary and testis sizes were identical.

There was a seasonal cycle in K (Fig. 6), which was higher between May and August than September to February. Apparently, white sea bream had high condition levels during spawning and post-spawning periods, as I_G declined, although K did not correlate with I_G (r_s, $n = 12$, $P = 0.96$).

RECRUITMENT

The overall densities of *D. sargus* caught during the beach-seine surveys at Porto Pim Bay averaged 41·6 individuals 1000 m^{-2}, with an average size of 4·1 cm L_T (Table III). Abundance peaked between May and July (80·2–250·9 individuals 1000 m^{-2}), corresponding to a substantial increase in catches of settlers and juveniles averaging in size from 2·1 to 4·2 cm L_T. From October to March, the fish were not abundant or absent. First settlers arrived by late May, when a large number (94%) of individuals <2·5 cm L_T were observed. The cohort could then be followed during the first year after settlement. After May, the majority of the individuals caught had a range of 2·1–4·0 cm L_T in June (87%), 2·6–6·0 cm in July (87%), 4·6–7·5 cm in September (85%), 6·1–10·0 cm in December (100%) and 8·6–15·0 cm in April (100%).
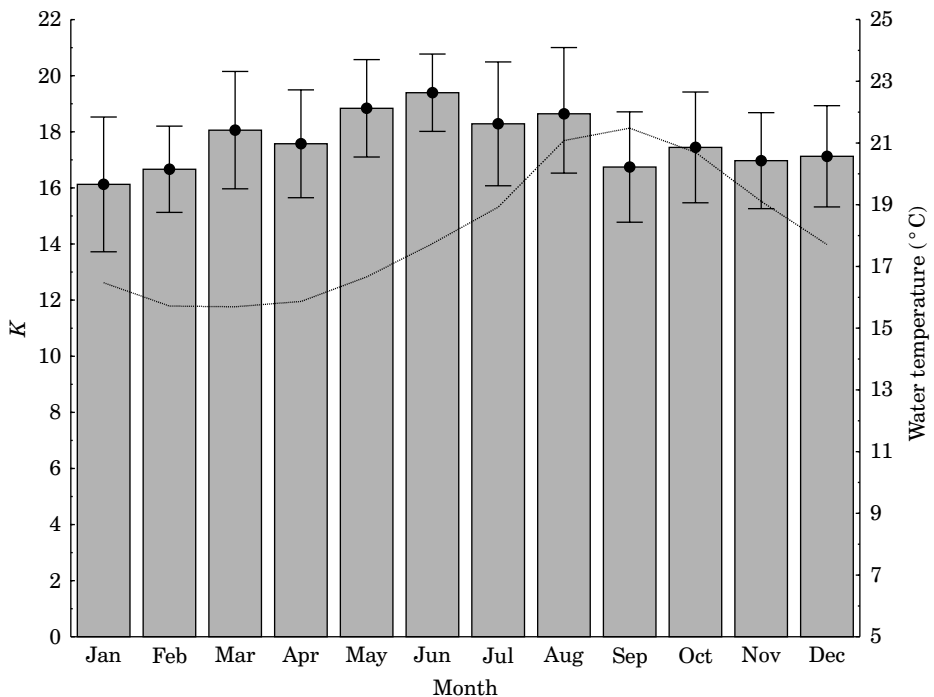

FIG. 6. Monthly mean ± S.D. Fulton's condition factor (▢) for mature *Diplodus sargus* (sexes pooled). Mean monthly sea temperature at 25 m depth (⋯⋯⋯) is also given.

TABLE III. Average number of *Diplodus sargus* caught in Porto Pim Bay, Faial Island, Azores, over the period 1997–1998. Each beach-seine had an estimated fishing area of 291 m^2

Month	Average number (per seine haul)	Average number (1000 m^{-2})	Average L_T (cm)	L_T range (cm)
January	0	0		
February	0·3	1·1	6·5	
March	0	0		
April[1]	5·0	17·2	11·0	8·7–14·9
May	23·3	80·2	2·1	1·4–17·9
June	73·0	250·9	3·3	1·7–14·5
July	47·7	163·8	4·2	1·6–16·2
August	0	0		
September	6·7	22·9	5·7	2·8–8·9
October	0·9	2·9	4·6	4·1–5·4
November	0·3	1·0	9·3	5·0–13·5
December	1·7	5·7	8·0	6·5–9·9
Total	12·1	41·6	4·1	1·4–17·9

[1]During 1998 two hauls were undertaken on 4 and 29 April. All white sea bream were caught during the second sampling.

DISCUSSION

REPRODUCTIVE BIOLOGY

Buxton & Garratt (1990) compared several sex change and rudimentary hermaphrodite sea bream species and identified distinctive characters for each of these two reproductive styles. These authors concluded that (1) size range (or length–frequency distribution), (2) mean size and (3) mean I_G of both sexes differed in sex change species. In the case of protandry, males should be smaller than females. Males and females should be similar in size for rudimentary hermaphrodite species. The present study revealed that the length–frequency distribution for males and females of *D. sargus* and the mean I_G during spawning months did not differ between sexes. Although females dominated the large size classes, thus attaining a greater mean size, the data suggest that the white sea bream is not a protandrous hermaphrodite.

The presence of intersex gonads in individuals <23 cm L_T, the abrupt decrease in male length–frequency distribution for 22 and 23 cm L_T classes and the corresponding increase in proportion of females in these length classes may indicate that some males retain the ability of changing sex into secondary females, and that such a sex change would preferentially take place in males of such size classes. These results appear to support the hypothesis that *D. sargus* in the Azores is a digynic species. If the digyny hypothesis is applicable, the observed overall sex ratio for the population (1 : 1·93) and the increase in proportion of females with size could be the result of some individuals in the population changing sex from males into secondary females. Alternatively, these patterns could be explained by at least two hypotheses: (1) patterns in sex ratio

and length distributions can reflect bias in the sampling method if sexes or different size classes occur in different areas or if their catchability to the sampling method is distinct. The vast majority of mature individuals, however, were caught by selective spearfishing following a stratified sampling design targeting equal sub-samples of individuals in different size categories. Therefore, this possibility does not seem to account for the observed patterns; (2) such patterns could have been related to differences in growth and mortality rates between sexes, where males experienced higher mortality than females. Preliminary estimates of growth ($k_{[females]} = 0.206$ years^{-1}; $k_{[males]} = 0.178$ years^{-1}; where k is the growth parameter of the von Bertalanffy growth function, unpubl. data) and mortality rates ($M_{[females]} = 0.515$ years^{-1}; $M_{[males]} = 0.462$ years^{-1}; Pauly, 1980) do not support this hypothesis. Furthermore, the annual sex ratio is also significantly biased towards females in other studies ($1 : 2.01$, Coetzee, 1986; $1 : 2.29$, Abou-Seedo *et al.*, 1990; $1 : 1.98$, Mann & Buxton, 1998). Therefore, the present results support the hypothesis that *D. sargus* is a digynic species, at least in its insular Azorean form.

Confirmation of the type of hermaphroditism exhibited in this species, mainly the distinction between late gonochorism (or rudimentary hermaphrodites) and digyny, should be ascertained with a detailed histological examination of gonadal development.

REGIONAL PATTERNS

Reproduction of temperate fishes is highly influenced by both photoperiod and temperature (Bye, 1984; Van Der Kraak & Pankhurst, 1996). The white sea bream seems to be no exception. The regional differences found in sexual maturity are consistent with changes in thermal regimes. Notably, it appears that as latitude decreases, both in the northern and southern hemispheres, the spawning season of *D. sargus* populations starts earlier and probably extends longer, highlighting the potential importance of temperature to the onset and duration of reproduction in this species (Table IV). This conclusion is supported by the analysis of very different thermal regimes, which vary from the cooler waters in the Gulf of Biscay and the Atlantic coast of South Africa (influenced by the cold Benguela Current) to the warmer coasts off the Azores, Kuwait and eastern South Africa (influenced by the warm Agulhas Current).

A particular aspect of the influence of temperature is its role as a cue to trigger reproductive activity. As previously noticed by Mann & Buxton (1998), spawning in *D. sargus* is promoted by favourable seawater temperatures and specifically triggered by changes in thermal regime. In the temperate areas of the Azores and north Spain, spawning started with the increase of seawater temperature immediately after the winter minimum. This behaviour was found to be remarkably consistent even over small distances within the sub-populations of the Azores archipelago (unpubl. data), which are subjected to minor annual changes in water temperature. This has been reported for other species (Monteiro *et al.*, 2001), and probably also occurs in other white sea bream populations. Access to monthly seawater temperature data in those regions would be valuable in testing such a prediction.

TABLE IV. Summary of spawning seasons and duration of spawning for different populations of *Diplodus sargus*. Temperature (° C) range during spawning and annual range in temperature are also presented. S.A., South Africa

| Site | Latitude | Spawning | | | Annual temperature range (° C) |
		Period	Duration (months)	Temperature range (° C)	
Asturias, Spain	43°N	Apr–Jun[1]	3	13–17[2]	12–21[2]
Azores, Portugal	38°N	Mar–Jun[3]	4	15–17[3]	14–24[3]
Lisbon, Portugal	38°N	Feb–May[4]	4		
Algarve, Portugal	37°N	Dec–May[5]	5		
Kuwait	29°N	Nov–Mar[6]	5		8 (Jan) to 35 (Aug)[6]
KwaZulu-Natal, S.A.	30°S	May–Nov[7]	7	17–20[8]	
Eastern Cape, S.A.	34°S	June–Dec[8]	7	17–20[8]	
South-east Cape, S.A.	34°S	Aug–Mar[8]	8	17–20[8]	

[1]Martínez-Pastor & Villegas-Cuadros, 1996; [2]Lavín & Cabanas, 2000; [3]present study; [4]F.J.O. Almada, unpubl. data, Faculdade de Ciências, Universidade de Lisboa; [5]Departamento de Oceanografia e Pescas, Universidade dos Açores, unpubl. data; [6]Abou-Seedo *et al.*, 1990; [7]Joubert, 1981; [8]Mann & Buxton, 1998.

RECRUITMENT

Nursery habitats are generally described as being areas where growth and survival of settled juveniles are enhanced (Gibson, 1994), or areas where post-settled juveniles fishes can persist and grow prior to first spawning (Steves *et al.*, 1999). Porto Pim Bay is a relatively undisturbed area providing a rare shallow water sandy habitat in the Azores. Such conditions make it an important nursery area for several fish species (Nash *et al.*, 1991, 1994*a,b*; Santos *et al.*, 1994; Santos & Nash, 1995) including the white sea bream. The results from the beach-seine surveys confirmed the importance of Porto Pim Bay as a nursery area for *D. sargus*.

White sea bream settled in the sheltered Porto Pim Bay from late May to July, the same period observed for the Mediterranean (Biagi *et al.*, 1998; Vigliola *et al.*, 1998). The cohort could be followed for the entire first year after settlement, however, the low abundance of individuals >7·5 cm L_T may indicate an emigration of individuals out of the nursery ground at *c.* 7·5 cm L_T starting in late July to early August. Additionally, the decline in abundance between June (250·9 individuals 1000 m^{-2}) and July (163·8 individuals 1000 m^{-2}) may indicate a combination of high mortality rates, which are typical during the first month after settlement, and early emigration (Macpherson *et al.*, 1997). Assuming a settlement size of 1·5 cm L_T, an emigration size of 6·0 cm L_T, and a daily growth of *c.* 0·57 mm day^{-1} (Planes *et al.*, 1999), the average time spent in the nursery should be *c.* 79 days. The estimates are consistent with those observed by Macpherson (1998) for the Mediterranean, however, growth and settlement size in the Azores may be substantially lower and thus, the estimated residence periods in nursery areas may be significantly higher. Changes in

habitat use with growth are a common phenomenon in both juveniles and adult fishes, and have already been described for *D. sargus* in the Mediterranean (Harmelin-Vivien *et al.*, 1995; Biagi *et al.*, 1998; Macpherson, 1998; Vigliola & Harmelin-Vivien, 2001). These ontogenetic shifts in habitat should be an adaptive response to reduce predation, enhance food availability and reduce competition (Macpherson, 1998).

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