Age, growth and reproduction of the axillary seabream, *Pagellus acarne*, in the Atlantic and Mediterranean waters off southern Spain

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The biology, growth and reproduction of the axillary seabream, Pagellus acarne*, was studied based on data obtained from the catches of the Andalusia commercial fleet operating off the coasts of southern Spain from October 2003 to September 2004. The axillary seabream had a very wide depth distribution, appearing from the surface down to 500 m depth. The length–weight relationship was given by TW = 0.0048 TL$^{3.3207}$ (R^2 = 0.98) (TW = total weight; TL = total length) for all fish from the Gulf of Cadiz and TW = 0.0093 TL$^{3.1132}$ (R^2 = 0.94) for all fish from the Alboran Sea. The proportion of females to males increases as length increases in both populations and the species is characterized by protandric hermaphroditism. Spawning males were present almost throughout the year although higher percentages were observed in spring and early summer. In females, the spawning period occurred mainly in spring. In both areas, the mean size at first maturity for males was smaller than for females. The mean lengths at first maturity were 18.04 cm for males and 21.7 cm for females from the Gulf of Cadiz, and 17.7 cm and 20.1 cm for males and females from the Alboran Sea, respectively. The average total fecundity was estimated at 290,070 and 173,509 oocytes for Atlantic and Mediterranean individuals, respectively. The parameters of the von Bertalanffy growth model were estimated by age readings of the 247 sagitta collected. Two rings, one opaque and one hyaline, were laid down each year on the otoliths. The opaque zone was formed during spring and summer and the hyaline one during the remaining months of the year. The relationship between otolith radius and total length of the fish was described by the equation: TL = 27.7 OR – 1.8 (r = 0.96) (where OR = otolith radius). The parameters of the fitted Von Bertalanffy growth equation were L$_\infty$ = 31.65 cm, k = 0.21 yr^{-1} in the Gulf of Cadiz and L$_\infty$ = 32.14 cm, k = 0.17 yr^{-1} in the Alboran Sea.*

Keywords: *Pagellus acarne*, age, growth, reproduction, maturity, Gulf of Cadiz, Alboran Sea

INTRODUCTION

Seabreams (Sparidae) are found in coastal waters worldwide and sustain important recreational and commercial fisheries (Fischer *et al.*, 1987). In the South Iberian region, seabreams are a dominant component of the continental shelf demersal fish community where more than 20 species are found (Baro, 1996; Baro & Serna-Quintero, 2000; Erzini *et al.*, 2001). One of these important species is the axillary seabream, *Pagellus acarne* (Risso, 1827). This demersal fish species inhabits various types of sea bottoms, especially seagrass beds and sand, down to 500 m depth (more commonly occurring between 40 and 100 m), the young are found closer to the shore (Bauchot & Hureau, 1986). The axillary seabream is a protandric hermaphrodite with sex inversion occurring

between 14 and 29 cm total length (TL) (Baro, 1996) and is considered very vulnerable to exploitation (Morato *et al.,* 2001). This species is widely distributed along the European and African coasts, from Denmark to Senegal and around the Macaronesia Islands, in the Mediterranean and in the Black Sea (Bauchot & Hureau, 1986).

Pagellus acarne is of high commercial importance and is targeted by the demersal fleets operating along the eastern Atlantic coasts and the Mediterranean Sea. In the eastern central Atlantic, the axillary seabream population is considered to be a single stock that is exploited by the high-seas cephalopod fishery, as well as the coastal and artisanal multispecies demersal fleets, not only by the coastal countries but also by the international fleet fishing in Morocco and Mauritania (FAO Fishery Committee for the Eastern Central Atlantic, 2003, 2004). Axillary seabream is one of the main target species of small-scale commercial fisheries in the northern Atlantic Algarve (Erzini *et al.,* 2001), Azores (Morato *et al.,* 2001) and Canary Islands (Pajuelo & Lorenzo, 1994, 2000). This species also represents a highly valued resource in the

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Mediterranean (Spedicato *et al.*, 2002). In the Gulf of Cadiz, several fishing techniques are used to fish sparids because of their high commercial value (Anonymous, 1994). In the northern Alboran Sea, *Pagellus acarne* is targeted by multispecies fisheries (bottom-trawl and artisanal fleets) and is considered the most important demersal fish species in terms of volume of catch and economic importance (Baro, 1996).

Total landings of seabreams in general, and of axillary seabreams in particular, have declined in recent years. In the Gulf of Cadiz, the landings decreased from a combined total of approximately 328 m per year in 1993 to less than 120 mt pear year from 2004 to 2007, representing a decrease of up to 60% (data obtained from the Spanish Institute of Oceanography database). In the Alboran Sea, landings have decreased from over 1500 mt pear year in 1985 (Gil de Sola, 1993) to less than 250 mt from 2004 to 2008 (data obtained from the Spanish Institute of Oceanography database), for a decrease of up to 80%. These trends have also been reported recently in other areas such as the Atlantic coast of Morocco (FAO Fishery Committee for the Eastern Central Atlantic, 2003, 2004), the Canary Islands (Pajuelo & Lorenzo, 2000) or the South of Portugal (Erzini *et al.*, 2001; Coelho *et al.*, 2005), making it necessary to establish management measures.

The study of some aspects of reproductive biology such as sexual differentiation and spawning season and the analysis of the evolution of maturity stages is important for assessment and management (Erzini *et al.*, 2001). Ageing and growth parameter estimation are also fundamental prerequisites for stock assessment. Knowledge of the rate of growth is essential for studies in population dynamics and knowledge of age structure is fundamental to determinate age at first capture and age at first maturity. The interest in axillary seabream for aquaculture has stimulated studies on its reproduction, feeding and growth (Greco *et al.*, 1995), and due to the economic importance of this fishery, it has been the focus of several studies in the recent past. Specifically, its biology has been studied in the Mediterranean (Andaloro, 1982), the Atlantic coast of Morocco and Western Sahara (Mennes, 1985; Lamrini, 1986), the Canary Islands (Pajuelo & Lorenzo, 2000) and the southern coast of Portugal (Santos *et al.*, 1995; Coelho *et al.*, 2005). However, there is scarce information available concerning the axillary seabream from the waters off southern Spain. Baro (1996) analysed aspects of the fishery and biology of this species in the northern Alboran Sea and these results constitute the only information available on the biology of *Pagellus acarne* in this area to date.

The objective of this paper is to study the age, growth and reproduction of two closed populations of axillary seabream separated by the Strait of Gibraltar, one from the Gulf of Cadiz (Atlantic southern coast of Spain) and the other from the Alboran Sea (Mediterranean southern coast of Spain). The present study also investigates the importance of the Strait of Gibraltar as a barrier between two marine biogeographical provinces, the Mediterranean Sea and the north-east Atlantic.

MATERIALS AND METHODS

Sampling

Monthly samples of *Pagellus acarne* were obtained from commercial catches landed by Andalusian fleets (75% bottom trawlers and 25% artisanal fleet, both gillnets and traps) in the ports of the Gulf of Cadiz (Sanlucar de Barrameda, Puerto de Santa Maria, Barbate and Tarifa) in the north-east Atlantic ($7°23' - 5°50'W$), and in the ports of the Alboran Sea (Algeciras, Estepona and Malaga) in the south-west Mediterranean ($5°50' - 2°11'W$) (Figure 1). In addition, samples were taken using a trawl net during the annual surveys in those areas. Axillary seabreams were sampled between October 2003 and September 2004. A total of 884 fish were analysed (477 from the Gulf of Cadiz and 407 from the Alboran Sea).

Specimens were measured for total length (TL) to the nearest 1 mm and weighed (total weight (TW) and eviscerated weight (EW) with a precision of 0.01 g. The gonad weight (GW) was recorded to the nearest 0.01 g, and the gonadosomatic index (GSI) was calculated as the percentage of gonad weight/eviscerated weight.

The parameters of the length–weight relationships were estimated by linear regression analysis on log-transformed data.

It was not possible to calculate the sex-ratio for the entire population because the sampling was non-random; therefore, we used data from past annual surveys to calculate the male: female ratio. 711 individuals captured in four annual surveys (1992–1995) were used for the Gulf of Cadiz, and data from 3373 individuals captured in two annual surveys (1990–1991) were used for the Alboran Sea. This study, however, analyses the proportion of males to females by size intervals. Statistically significant deviations of a null
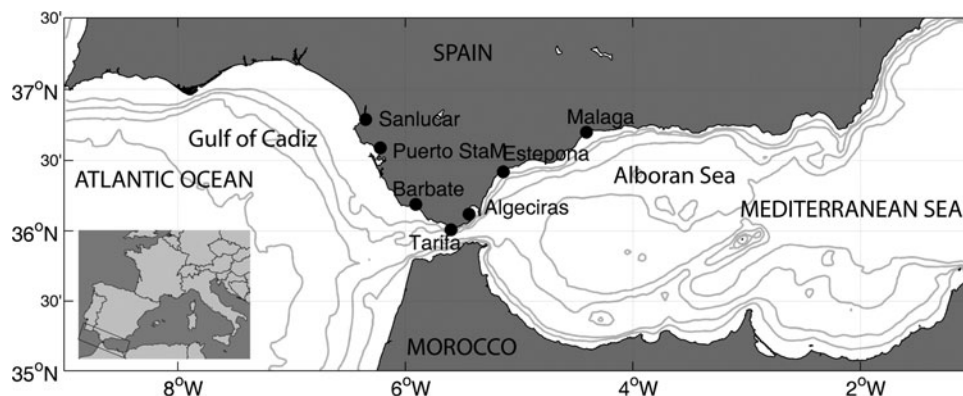

Fig. 1. Location of the study area. The ports in the Gulf of Cadiz were Sanlucar de Barrameda, Puerto de Santa Maria, Barbate and Tarifa, and the ports in the Alboran Sea were Algeciras, Estepona and Malaga.

hypothesis (proportion 1:1) were tested by χ^2 in those size intervals with ten or more individuals.

Reproduction

For the histological examination of reproductive organs, 867 gonads were dissected (461 from the Gulf of Cadiz and 406 from the Alboran Sea), fixed in 10% phosphate buffered formaldehyde (pH 7.2) for 24 hours, dehydrated with increasing concentrations of ethanol and embedded in paraffin wax. Gonads were sectioned in cross-sections (3 μm thickness) and stained with haematoxylin–eosin and haematoxylin–VOF (Gutiérrez, 1967). Histological sections were reviewed under a light microscope and micrographs were taken. The specimens of axillary seabream were separated into the following groups: females (with ovaries or ovotestes with functional ovary), males (with ovotestes with functional testes), hermaphrodites (with ovotestes at the same maturity stage) and indeterminate (with unidentifiable gonads). The sex was recorded for each fish sampled and the gonads were examined microscopically to determine the maturation state. The oocytes were sorted according to the histological features described by Mandich et al. (2002). Each ovary was classified into distinct maturation stages based on the presence and absence of different types of oocytes and the most advanced oocyte stage present in the ovary. Based on these characteristics, five distinct stages of ovarian maturation were proposed: (I) previtellogenic; (II) vitellogenic; (III) maturation; (IV) spawning; and (V) post-spawning. Classification of the testes was based on the gonad development criteria described by Micale et al. (2002), modified for this species into a five-stage scale: (I) immature/resting; (II) developing; (III) mature; (IV) spawning; and (V) recovering spent/post-spawning. Testes were classified according to the male germ cell stages present in the testis and the presence and development of sperm within the sperm sinuses.

The size of sexual inversion was calculated following Shapiro (1984) during the reproductive season. Size at first sexual maturity (L_{50}) was defined as the size at which 50% of males and females become mature (Batts, 1972) and was estimated using specimens collected during the months of reproductive activity. The percentage of mature individuals was estimated for size intervals of 1 cm and sex, and the data were fitted with a non-linear regression. The logistic curve used was $Y = 1/[1 + e^{-k\,(L-L50)}]$ where Y is the proportion of mature individuals in each size interval, L the mean length of the interval, and k the constant of the logistics function. To evaluate the differences in size at first maturity between sexes the variance of the L_{50} of each sex was calculated. Assuming that L_{50} estimates are normally distributed, then the Z statistic can be computed as: $Z = [(a_1/b_1) - (a_2/b_2)]/[\sqrt{(V_1 + V_2)}]$ where a_i and b_i are the logistic regression coefficients and V_i the L_{50} variances of each sex compared. Z values can be used to test the null hypothesis of parameter equality (Gunderson, 1977).

Stereological methods (Weibel, 1979) were applied to estimate total and relative fecundity using histological sections of ovaries in stage II and stage III of maturation with the help of image analysis. Several images from different fields of each histological section were captured and digitized. Gonads with postovulatory follicles were not appropriate for fecundity estimation because such females were considered to have begun to spawn at the time of sampling. Thus, these specimens were excluded from the fecundity estimation. Total fecundity was defined as the total number of vitellogenic or advanced yolked oocytes at any time in the ovary (Hunter et al., 1992). Relative fecundity was calculated for each organism as total fecundity divided by eviscerated weight. To establish the relation between the total fecundity (Y) and eviscerated weight, total length or gonad weight of the fish, regression analyses were carried out to adjust, in each case, the data to two models: linear ($Y = a + bX$) and power ($Y = aX^b$), where Y is the total fecundity, X is TL, TW or GW; and a and b are parameters of the equation.

Age and growth

Sagittal otoliths from 247 specimens were used for age determination. Whole otoliths were immersed in a 30% aqueous solution of glycerine for 2 hours, prior to being read under reflected light, on a black background. Two readings from two independent readers were carried out for each otolith. Whenever there was a discrepancy between the four readings, the age data were excluded from the study. The criteria used to determine age were: (1) the date of birth was considered to be 1 June according to the reproduction season (summer) observed in this study; (2) each year a translucent and an opaque growth band are deposited on the otolith; and (3) the age of the fish corresponds to the number of complete translucent bands (n). Monthly proportions of opaque and translucent bands along the edge of the otoliths were examined in order to validate the annual periodicity of band formation. The fact that the formation of the rings was regular implied that the otoliths could, therefore, be used to determine growth. Apart from the number of annuli on each otolith, the otolith radius (OR) (distance from the focus to the otolith posterior end) and the type of marginal formation were also recorded. The measurements were determined using image analysis (Program Visilog 6 + TNPC 3.2, described by IFREMER). The back-calculation method reconstructs the size of individuals at a younger age, based on growth recorded in their calcified structures (Casselman, 1987). An age–length key was constructed. Whole length distributions by age were used to estimate the growth rate of axillary seabream. The parameters of the von Bertalanffy equation for the pooled data of both sexes from each sampling area were estimated by using the program FISAT II. The total length distribution by age-class was fitted to the von Bertalanffy equation. $L_t = L_\infty[1 - \exp(-k(t - t_0))]$. In this equation, L_t is the mean fish length at age t; L_∞, k and t_0 the parameters that determine the shape of the growth curve. L_∞ is defined as the asymptotic mean length; k the rate at which the curve approaches the asymptote and t_0 the age at which mean length is zero. All the parameters were calculated using FISAT II (Gayanillo et al., 1993). Growth curves were compared with other studies using the phi-prime test (Φ') following Munro & Pauly (1983), where $\Phi' = \log_{10} k + 2 \log_{10} L_\infty$. A nested ANOVA was carried out to detect differences in growth between the areas of study following Sokal & Rohlf (1995).

RESULTS

Sample characteristics

The overall ratio of males to females was 1.7:1 in the Gulf of Cadiz and 1.5-2.2:1 in the Alboran Sea.

Of the total number of axillary seabream examined in the Gulf of Cadiz, there were 206 males, 200 females, 48 hermaphrodites and 5 indeterminate. The range of the total lengths of the fish sampled was 11.3–30.9 cm (mean length = 22.9 cm, SD = 3.2 cm). The proportion of males and females grouped into 2 cm length intervals significantly deviated from the expected 1:1 ratio (χ^2-test, $P < 0.05$) for most size categories, with the exception of lengths between 20 and 22 cm (Figure 2A). Males predominated in smaller size intervals (range TL 13–27 cm, mean TL 22.7 cm, SD = 2.8 cm), whereas most females were equal to or larger than 25 cm (range TL 19–31 cm, mean 24.3 cm, SD = 2.4 cm). Hermaphrodites made up 10.6% of the specimens examined and were observed in smaller and intermediate sizes (11–27 cm).

Of the 405 specimens examined in the Alboran Sea, there were 174 males, 175 females, 56 hermaphrodites and 2 indeterminate. The range of TL was 10.7–29.4 cm (mean length = 21.8 cm, SD = 2 cm). Although the proportion of males seems to decrease as length increases (range TL 15–27 cm, mean TL 21.5 cm, SD = 1.9 cm), and the females ranged between 17 and 29 cm (mean TL 22.4 cm, SD = 1.8 cm), the χ^2 test showed that there were no significant differences except in the 18–20 cm and 22–24 cm ranges. Hermaphrodites were present in all size intervals except in the range between 26 and 28 cm (Figure 2B).

In both areas, hermaphrodites were present only during the period of sexual repose, maturing as males or females during the spawning season.

The parameters of the total length–total weight relationship are given in Table 1 where positive allometry can be

Table 1. Parameters of total length (mm)–total weight (g) relationship.

Area	Sex	a	b	N	R^2
Gulf of Cadiz (north-east Atlantic)	Males	0.0051	3.3049	194	0.98
	Females	0.0090	3.1192	195	0.94
	All fish	0.0048	3.3207	461	0.98
Alboran Sea (south-west Mediterranean)	Males	0.0126	3.0124	173	0.92
	Females	0.0113	3.0539	174	0.90
	All fish	0.0093	3.1132	406	0.94

N, number.

observed. In both sampled areas, there was no significant difference in the allometric coefficient of the regression between the sexes (ANOVA for comparison of regression lines, $P > 0.1$), so data can be pooled. However, the analysis between areas showed that there were significant differences in the regression coefficients for males (ANOVA for comparison of regression lines, $P < 0.05$) but not for females ($P > 0.1$).

Reproduction

SPAWNING PERIOD

In the Gulf of Cadiz, the previtellogenic females appeared from December to March and August to October (Figure 3A). After these periods, the females began to develop the gonads and were present in vitellogenic and maturation stages successively. Females at the spawning stage were collected in autumn, spring and the beginning of summer, although they occurred in higher quantities between April and June. However, spawning males were present in every sampled month, although higher percentages were observed in autumn, spring and early summer (Figure 3B). It is significant to note the scarce number of resting, developing and mature males. Males with post-spawning testes were collected during the same periods as the females but higher percentages were observed one month later.

Maximum values of the gonadosomatic indices were found from April to June in both sexes (Figure 3A, B), when there was a maximum occurrence of spawning specimens, corresponding to the peak of the spawning season. The mean GSI for females was lowest at the previtellogenic and vitellogenic stages of the ovary, and for males with post-spawning testes. For both sexes, minimum values were observed from December to March and August.

In the Alboran Sea, previtellogenesis started in September and continued until May, although peaks were observed from December to February (Figure 3C). The higher percentage of females with vitellogenic ovaries was observed in March and April. Finally, females at maturation and spawning stages were collected in summer and the beginning of autumn. Few resting males were present from January to March and in August, and developing males were also present in these months (Figure 3D). Males reached maturity in March and September. Spawning males were present almost throughout the year, although the highest percentage was observed from May to October.

Peaks in gonadosomatic indices, both in females and males, coincided with the spawning period as determined by changes in stages of maturity (Figure 3C, D). The highest values of the GSI for both sexes occurred between May and October, with a maximum in June. The values were low and remained almost
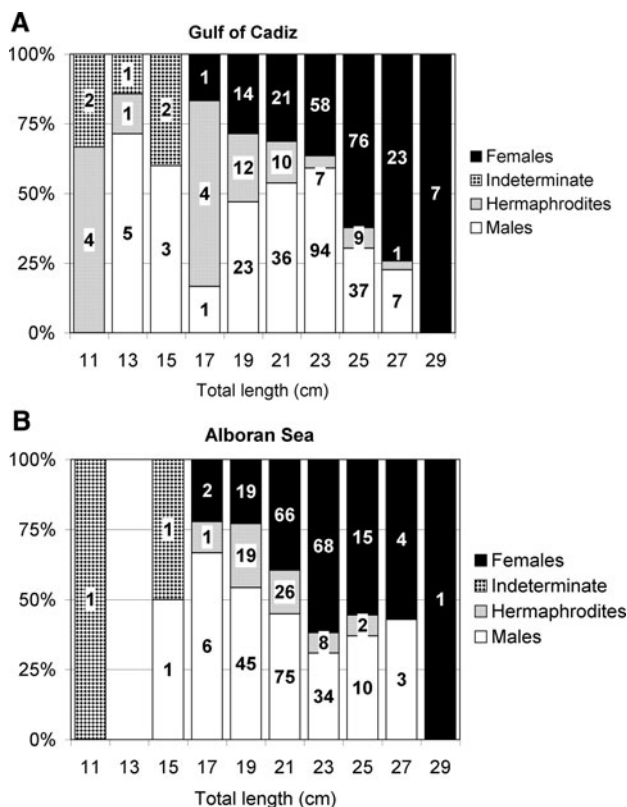

Fig. 2. Length–frequency distributions for males, females and hermaphrodites by size intervals in the two study areas: (A) Gulf of Cadiz, and (B) Alboran Sea. Number of individuals (*N*) is indicated inside the columns.
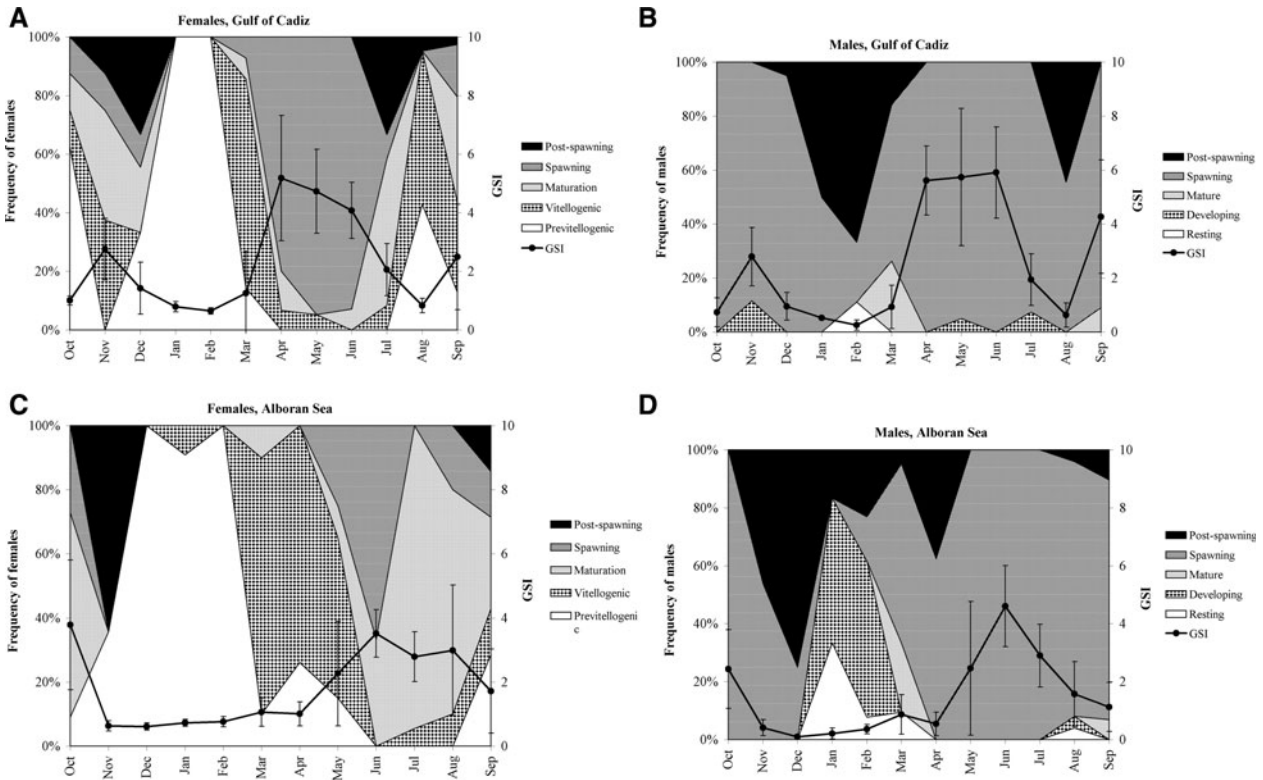
Fig. 3. Monthly variation in the average of the gonadosomatic index (GSI) and monthly changes in the per cent frequency of the maturity stages of gonads for females (A) and for males (B) of *Pagellus acarne* from the Gulf of Cadiz and for females (C) and for males (D) from the Alboran Sea. Bars indicate standard deviation.

unvaried from November to April, corresponding with the months of decreased reproductive activity and rest of the gonads.

SIZE OF SEXUAL INVERSION AND SIZE

AT SEXUAL MATURITY

The range of lengths where both males and females were found in the same length-class was quite wide for this species. Estimated size of sexual inversion was 23.5 cm in the Gulf of Cadiz (overlap range between 20.5 and 26.5 cm) and 21.5 cm in the Alboran Sea (overlap range between 18.5 and 26.5 cm).

Differences in size at maturity were observed between males and females from the Gulf of Cadiz (Figure 4A), where estimated L_{50} was 21.7 cm for females and 18.04 cm for males. A significant difference in L_{50} (z-test, $P < 0.05$) was found between both sexes. Estimates of size at first maturity and parameters of the logistic equation fitted for females and males from the Gulf of Cadiz are summarized in Figure 4A. The data for the estimation of length at sexual maturity for females and males provided a good fit ($r^2 = 0.96$ and 0.93, respectively).

The sexual maturity curves for females and males from the Alboran Sea are shown in Figure 4B. The estimated length at
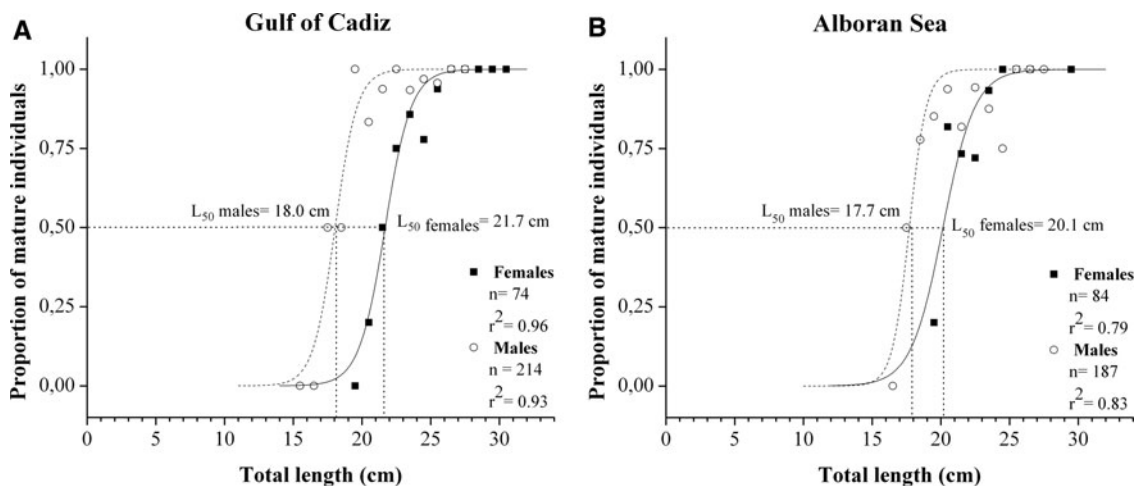

Fig. 4. Sexual maturity curves for females and for males of *Pagellus acarne* from the Gulf of Cadiz (A) and the Alboran Sea (B). Parameter estimates and L_{50} obtained from the maturity analyses of males and females are shown.

which 50% of the females in the population reached sexual maturity was 20.1 cm, and 17.7 cm for males, with significant differences (z-test, $P < 0.05$).

ESTIMATION OF FECUNDITY

Fourteen females from the Gulf of Cadiz were analysed to estimate total fecundity (Table 2). These estimates came from axillary seabream ranging in total length from 20.9 to 28.2 cm, eviscerated weight from 112.0 to 277.4 g, and gonad weight 0.59 to 16.56 g. Total fecundity estimates reached values ranging from 19,417 to 641,957 oocytes (mean = 290,070; SD = 196,617). Relative fecundity showed a wide variation among females. The maximum and minimum was 106 to 2314 oocytes per gram of individual respectively, with an average of 1314 ± 667 oocytes per gram of individual.

Regression analysis showed significant positive correlation between total fecundity and total length (ANOVA $P < 0.01$), eviscerated weight (ANOVA $P < 0.01$) and gonad weight (ANOVA $P < 0.01$). The models are shown in Table 3. In all cases, the best fit was obtained with the linear model. A comparison of determination coefficient reveals that the relationship between total fecundity and gonad weight was more significant ($r^2 = 0.98$, $P < 0.01$) than that of fecundity and eviscerated weight ($r^2 = 0.80$, $P < 0.01$) or fecundity and total length ($r^2 = 0.76$, $P < 0.01$).

In the Alboran Sea, maximum fecundity (783,114 oocytes) was observed in a specimen with a total length of 29.4 cm and eviscerated weight of 354 g, and the minimum fecundity (35,752 oocytes) was observed in a specimen with a total length of 23 cm and 173 g eviscerated weight (Table 2). The average total fecundity was $173,509 \pm 183,076$ oocytes. Relative fecundity varied between 207 and 2210 oocytes per gram of individual (mean = 954; SD = 575).

Table 3 shows a significant correlation between all measured parameters and total fecundity, although the highest coefficients were observed between total fecundity and gonad weight ($r^2 = 0.93$, $P < 0.01$), followed by eviscerated weight ($r^2 = 0.71$, $P < 0.01$) and total length ($r^2 = 0.66$, $P < 0.01$). The best relationship between total fecundity and gonad weight was expressed by the power equation.

However, the relationship between total fecundity and eviscerated weight and the equation between total fecundity and total length were linear.

The null hypothesis (total fecundities from the two areas had the same mean) was accepted (ANCOVA, F = 1.94; $P = 0.1759$).

Age and growth

The otoliths showed a seasonal variation in the formation of hyaline and opaque zones during the period of the study (Figure 5). Rapid-growth rings (opaque) were formed mainly in summer–autumn and slow-growth rings (hyaline) were more frequent in winter–spring. The observation and interpretation of the otoliths had a success rate of 73%, based on the independent and concordant readings of 2 different observers. The relationship between otolith radius (OR) and fish length, both in mm, was established. The slopes of the total length and OR regression did not differ between sexes or sampling areas (ANOVA for comparison of regression lines, $P > 0.1$). The relation is given by equation: TL = 27.7 OR – 1.8 (r = 0.96). Fish length and otolith size were closely correlated ($r^2 = 0.93$). The proportionality between fish growth and increase in otolith size allowed the use of back-calculation for determining growth.

Full agreement was obtained in the age readings of 247 otoliths. Axillary seabreams aged I up to VII years were present in the samples (Table 4), where 12 was the maximum age observed. The calculated theoretical maximum length value for the Gulf of Cadiz (31.6 cm) is close to the size of the largest fish sampled, while the theoretical maximum length value for the Alboran Sea is higher than the length of the largest fish in this area (because of the lack of individuals older than 7 years, the L_∞ used is the one calculated by Baro (1996) 32.14 cm for the Alboran Sea). During the first year of life, fish attain nearly 50% of their theoretical maximum length in both sampling areas.

The von Bertalanffy growth curves are shown in Figure 6. The phi-prime (Φ') test estimations present similar values:

Gulf of Cadiz: $L_\infty = 31.65$ cm, $k = 0.21$ yr^{-1}, $t_0 = -1.76$ yr and $\Phi' = 2.32$.

Table 2. Total and relative fecundity of *Pagellus acarne* from the Gulf of Cadiz and Alboran Sea.

Gulf of Cadiz (N = 14)					Alboran Sea (N = 15)				
TL	EW	GW	Total fecundity	Relative fecundity	TL	EW	GW	Total fecundity	Relative fecundity
20.9	112.0	1.300	64,588	577	20.8	116.7	4.277	177,846	1524
23	135.8	3.803	171,452	1263	21	122.1	1.687	89,782	735
23.8	182.5	0.591	19,417	106	21.4	120.2	5.541	173,331	1442
23.9	167.4	5.491	149,793	895	21.6	134	1.335	61,666	460
24.2	180.0	2.215	90,314	502	21.7	137.4	1.283	47,979	349
25	172.8	3.594	131,658	762	21.7	128	6.807	229,883	1796
25.4	202.4	9.411	284,815	1407	22.2	149.6	3.060	153,536	1026
26	195.0	8.156	287,787	1476	22.4	141.4	2.310	106,259	751
26.5	203.0	7.537	280,498	1382	22.6	164.1	3.177	119,247	727
27.2	259.1	14.780	524,217	2023	22.7	153.1	2.324	132,315	864
27.2	242.1	14.850	433,724	1792	23	173	1.016	35,752	207
27.2	235.0	14.271	495,968	2111	23.4	186.6	3.592	124,903	669
27.8	277.4	16.564	641,957	2314	23.8	168.9	1.726	65,104	385
28.2	270.2	13.944	484,790	1794	26.7	259.1	10.514	301,923	1165
					29.4	354.3	16.214	783,114	2210

TL, total length (cm); EW, eviscerated weight (g); GW, gonad weight (g); N, number.

Table 3. Linear and power models used to express the relation between total fecundity and total length (TL) or eviscerated weight (EW) or gonad weight (GW) of *Pagellus acarne* from the Gulf of Cadiz and the Alboran Sea. Significant relationship between total fecundity and each of the measured parameters (TL, EW and GW) was found using analysis of variance (ANOVA), 'a' and 'b' = estimated parameters; r^2 = determination coefficient; S = significant at $P < 0.01$; S* = significant at $P < 0.05$.

	Relationship	Linear				Power			
		a	b	r^2	$P < 0.01$	a	b	r^2	$P < 0.01$
North-east Atlantic	Fecundity and TL	$-2.0 \cdot 10^6$	$8.2 \cdot 10^4$	0.76	S	$4.0 \cdot 10^{-8}$	9.08	0.62	S
	Fecundity and EW	$-4.3 \cdot 10^5$	$3.6 \cdot 10^3$	0.80	S	0.186	2.64	0.49	S
	Fecundity and GW	$6.5 \cdot 10^3$	$3.4 \cdot 10^4$	0.98	S	$3.9 \cdot 10^4$	0.94	0.97	S
South-west Mediterranean	Fecundity and TL	$-1.0 \cdot 10^6$	$6.5 \cdot 10^4$	0.66	S	0.025	4.94	0.35	S*
	Fecundity and EW	$-2.3 \cdot 10^5$	$2.4 \cdot 10^3$	0.71	S	110.9	1.39	0.29	S*
	Fecundity and GW	$-8.9 \cdot 10^3$	$4.2 \cdot 10^4$	0.92	S	$4.4 \cdot 10^4$	0.93	0.93	S

Alboran Sea: $L_\infty = 32.14$ cm (Baro, 1996), $k = 0.17$ yr^{-1}, $t_0 = -2.69$ yr and $\Phi' = 2.24$.

The nested ANOVA showed no differences in growth between axillary seabream from the Gulf of Cadiz and from the Alboran Sea ($P = 0.935$).

DISCUSSION

The positive allometry of the total length–total weight relationship was also observed for the species in other studies (Pajuelo & Lorenzo, 1994, 2000; Santos *et al.*, 1995; Coelho *et al.*, 2005). Differences between males and females in the length–weight relationship are explained by the different size distributions of the two sexes as a consequence of the protandric hermaphroditism. These differences had already been described by Pajuelo & Lorenzo (2000).

The sex-ratio of 1.7–2:1 in favour of males is similar to that obtained by Arculeo *et al.* (2000). The spawning period of axillary seabream in the study areas extended from the end of spring to early autumn with a peak in the summer months, while the resting period occurred mainly during the winter months. These results agree with previous reports (Andaloro, 1982; Lamrini, 1986; Santos *et al.*, 1995; Baro, 1996; Arculeo *et al.*, 2000; Coelho *et al.*, 2005), with the exception of Pajuelo & Lorenzo (2000) in the Canary Islands and Le-trong & Kompowsky (1972) on the north-west African coast, where there seems to be a tendency for this species to

spawn between winter and spring in low latitudes and later in the year in higher latitudes. The temperature appears to be the most important environmental factor influencing the reproduction of fish (Wootton, 1990). On the other hand, this long reproductive period in the Gulf of Cadiz and the Alboran Sea is similar to the results obtained by Coelho *et al.* (2005) on the south coast of Portugal and Baro (1996) in the Alboran Sea. The gonadosomatic index shows that this species spawns 1 or 2 months earlier in the Gulf of Cadiz than in the Mediterranean, as Santos *et al.* (1995) pointed out.

The present study revealed that males reached sexual maturity at a smaller size (approximately 3 cm) than females, which seems to be a characteristic of protandric species. Likewise, individuals from the Gulf of Cadiz reached first maturity at a larger size than those in the Alboran Sea. Lamrini (1986) reported that the axillary seabream on the north-west African coast reached first maturity at a total length of 20.9 cm. Later, Santos *et al.* (1995) obtained the same size at first maturity for females from south Portugal and 19.7 cm for males. Our results agree with these authors. However, the size at first maturity in this study is higher than the results obtained by other authors such as Pajuelo & Lorenzo (1994, 2000) in the Canary Islands and Coelho *et al.* (2005) in the south of Portugal. In the Mediterranean Sea, Andaloro (1982) observed a size at sexual maturity of 16.5 cm for males and females, while Baro (1996) reported 19 cm for both sexes. These lengths at first maturity were
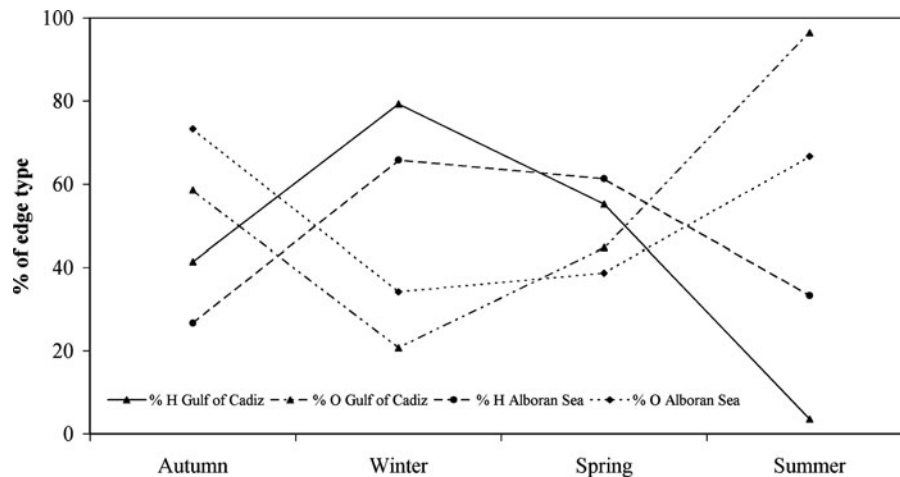

Fig. 5. Evolution of the occurrence percentage of edge type in otoliths in both areas of study.

Table 4. Length–age key of the axillary seabream in the two sampling areas.

| Total length (cm)	Age-classes														
	Gulf of Cadiz								Alboran Sea							
	0	I	II	III	IV	V	VI	VII+	0	I	II	III	IV	V	VI	VII +
<11.0	3	1							1							
12.0	4	2														
13.0		1														
14.0		4														
15.0		3	1							1						
16.0		2	3								2					
17.0			4	1							3	1				
18.0		1	4	2							4					
19.0		1	5	3							9	6	3	1		
20.0		2		2	2						6	5	2			
21.0			3	7	1						3	8	3	1		
22.0			5	5	2							10	7			
23.0			1	2	5	3						2	5	3		
24.0				6	10	1						1	4	5	2	1
25.0					5	1	5						3			1
26.0					5	8	2					1	1		2	1
27.0					1	1	3									1
28.0							2									
29.0							1									
30.0							2									
N	7	17	21	22	19	26	11	15	1	1	27	34	28	10	4	4
Mean	11.9	15.6	18.8	21.3	23.1	24.8	26.2	27.2	10.7	15.6	19.2	21.4	22.8	23.3	25.5	26.6

N, number.
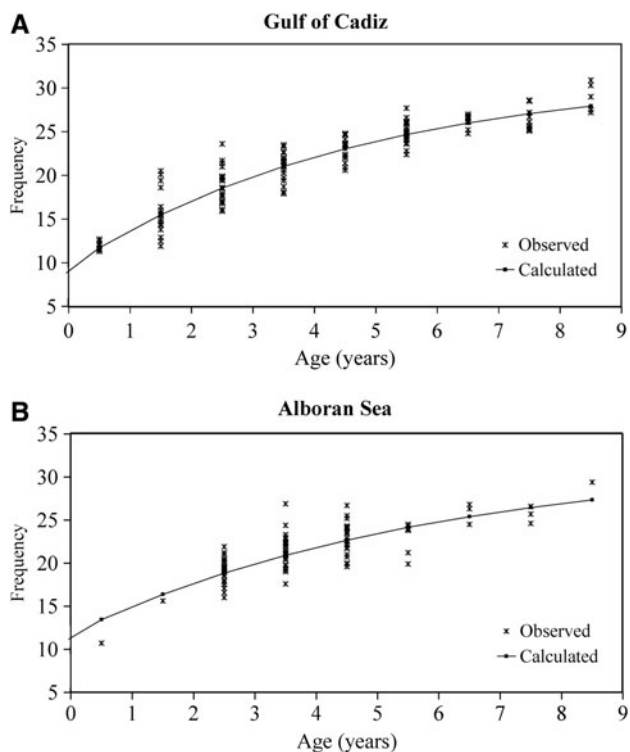
Fig. 6. Von Bertalanffy growth curves for all individuals of *Pagellus acarne* off the Andalusian coast obtained from otolith readings from the Gulf of Cadiz (A) and the Alboran Sea (B).

smaller than those found in the Alboran Sea, where males were sexually mature at 17.7 cm and females at 20.1 cm.

There are few references in the literature regarding the fecundity of *P. acarne*, apart from Le-trong & Kompowsky (1972) for the north-west African coast and Baro (1996) for the Alboran Sea. Le-trong & Kompowsky (1972) estimated that total fecundity ranged from 85,000 to 536,000 oocytes, values similar to our results. However, Baro (1996) estimated batch fecundity based on counts of hydrated oocytes and, consequently, it is difficult to compare our results. The use of this method could explain why the values of fecundity obtained by this author were lower than our results. However, this author wrote about the possibility that if all the yolked oocytes were spawned, the total fecundity could be between 70,000 and 500,000 oocytes. This possible result would concur with our study. Compared to other species of the same genus, the total fecundity of *P. acarne* in the present study is somewhat higher than the results estimated for *P. erythrinus* by Larrañeta (1964) and lower than that estimated for *P. bogaraveo* by Krug (1990, 1998). These differences between species may be partly due to differences in oocyte size.

The observation and interpretation of the otoliths for the axillary seabream is considered to be adequate and consistent for estimating ages of this species (Erzini *et al.*, 2001; Coelho *et al.*, 2005; Abecasis *et al.*, 2008). Previous studies have used otoliths to age *P. acarne* (Andaloro, 1982; Baro, 1996; Pajuelo & Lorenzo, 2000; Erzini *et al.*, 2001; Coelho *et al.*, 2005).

The marginal increment analyses in the otoliths showed that a pair of bands (one opaque and one hyaline) was deposited with an annual periodicity, with the opaque bands more frequent during summer and autumn. This analysis validated the use of otoliths for assessing age in this species. The same annual pattern had already been observed for this species in

the south of Portugal where the opaque band was deposited mainly in summer (Erzini *et al.*, 2001; Coelho *et al.*, 2005) and in the Canary Islands where the opaque bands were formed between May and August (Pajuelo & Lorenzo, 2000).

The von Bertalanffy growth curve fitted to otolith based age–length data explains the growth pattern for the observed size-range of axillary seabream. The relative low value of k is characteristic of a slow growing, long lived species. In this study, the oldest observed fish was 12 years old, although age-classes above 7 years are poorly represented in the landings. The zero age-class is not represented because individuals smaller than 15 cm were not found in the markets. In the Mediterranean, Andaloro (1982) found that individuals of this species can reach an age of 8 years, while in the Atlantic, Pajuelo & Lorenzo (2000) found axillary seabreams up to 10 years old in the Canary Islands and Erzini *et al.* (2001) found an 18-year-old specimen in the south of Portugal. The fitted growth model probably does not properly describe juvenile growth in this species because of the lack of individuals smaller than 14 cm in the sample, due to the nature of the sampling itself (commercial fishing vessels are not allowed to fish this species under 17 cm).

The k values estimated at 0.21 for the Gulf of Cadiz and 0.17 for the Alboran Sea are close to the k values reported by Mennes (1985) for Morocco and Erzini *et al.* (2001) for the south coast of Portugal, although they are lower than the ones reported by other authors (Andaloro (1982) estimated $k = 0.32$ for females and $k = 0.42$ for males for the Mediterranean; Pajuelo & Lorenzo (1994) estimated a k value of 0.23 for the Canary Islands). The estimated value of L_∞ of 31.65 cm in the Gulf of Cadiz is similar to the L_∞ estimated by Baro (1996) for the Alboran Sea. Both Pajuelo & Lorenzo (1994) for the Canary Islands and Erzini *et al.* (2001) for the south coast of Portugal calculated a L_∞ of 32 cm, similar to the value obtained in our study, while Andaloro (1982) estimated a value of L_∞ of 26.2 cm for males and 29.8 cm for females. The calculated values are reasonable, given the maximum observed length of 30.9 cm in the north-west Atlantic and 29.4 cm in the Alboran Sea.

Differences between growth of axillary seabream in the Gulf of Cadiz and the Alboran Sea were not observed, according to the results of a nested ANOVA. Because this species is a protandric hermaphrodite in the study area, males appeared mostly in the lower length-classes and the females in the higher ones. This type of hermaphroditism had previously been described for this species (Alekseev, 1967; Andaloro, 1982; Lamrini, 1986; Pajuelo & Lorenzo, 1994, 2000; Baro, 1996; Arculeo, 2000; Erzini *et al.*, 2001; Coelho *et al.*, 2005), and explains why individuals are mainly male in the earlier years of life and mainly female in the later years, as well as the presence of individuals with ovotestes. Sexual inversion should occur between 20 and 26.5 cm (between 3 and 6 years of age), very similar to that described by Erzini *et al.* (2001) or Coelho *et al.* (2005) in the Algarve (length of 20–24 cm, between 3 and 6 years old), but at older ages than those observed by Pajuelo & Lorenzo (1994) for the Canary Islands. Baro (1996) observed a wider range of lengths of sexual inversion (between 14 and 29 cm) in the Alboran Sea.

The phi-prime test (Φ') estimates provide an indication of estimation reliability, since it has been suggested that phi-prime values are similar for the same species and genera (Bellido *et al.*, 2000). The results obtained in the present study are very similar to those found in other areas of

distribution of *P. acarne* (Andaloro, 1982; Mennes, 1985; Pajuelo & Lorenzo, 1994, 2000; Baro, 1996; Erzini *et al.*, 2001; Coelho *et al.*, 2005; Abecasis, 2008).

In Spain, current legislation for *Pagellus acarne* stipulates a minimum landing size of 17 cm from communitarian waters (Regulation CE 1967/2006, DOCE L409) and 12 cm from national waters (Regulation RD 560/1995, modified by RD 1615/2005) in the south-east Mediterranean ports. Management of axillary seabreams is based on minimum landing sizes, minimum mesh sizes, protection of juvenile areas and regulation of effort. Due to the special life-history characteristics of protandric hermaphrodites, where both males and females reach sexual maturity at sizes larger than the allowed minimum size of capture in the northern Alboran Sea, and because of the alarming decrease in landings of this species in the area of study, we believe current regulation may not be appropriate and minimum landing size for this species should be increased as a precautionary measure on the basis of accurate maturity data. Another problem is that no minimum size exists for landing in the Gulf of Cadiz. In order to preserve the stock in the Gulf of Cadiz, an appropriate minimum landing size should be established for this species in this area.

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REFERENCES

Abecasis D., Bentes L., Coelho R., Correia C., Lino P.G., Monteiro P., Gonçalves J.M.S., Ribeiro J. and Erzini K. (2008) Ageing seabreams: a comparative study between scales and otoliths. *Fisheries Research* 89, 37–48. doi: 10.1016/j.fishres.2007.08.013

Alekseev F.E. (1967) *Hermaphroditism and regulation of population sexual structure in* Pagellus acarne *(Risso, 1826)*. ICES C.M. 1967/G:7, 4 pp.

Andaloro F. (1982) Résumé des paramètres biologiques sur *Pagellus acarne* de la mer Tyrrhénienne méridionale et de la mer Ionienne septemtrionale. *FAO, Fisheries Report* 266 (Annexe M), 89–92.

Anonymous (1994) *Las artes de pesca en el litoral gaditano.* Cadiz: Excma. Diputación Provincial de Cadiz.

Arculeo M., Brusle'-Sicard S., Potoschi A. and Riggio S. (2000) Investigations on gonadal maturation in *Pagellus acame* (Pisces, Sparidae) in the Strait of Messina (Sicily). *Italian Journal of Zoology* 67, 333–337.

Baro J. (1996) *Biología pesquera del besugo* [Pagellus acarne *(Risso, 1826)] del Mar de Alboran.* PhD thesis. University of Málaga, Málaga, Spain.

Baro J. and Serna-Quintero J.M. (2000) Asociaciones de espáridos en el golfo de Cadiz: distribución espacial. *Thalassas* 16, 33–39.

Batts B.S. (1972) Sexual maturity, fecundity and sex ratios of the skipjack tuna, *Katsuwonus pelamis* (Linnaeus), in North Carolina waters. *Transactions of the American Fisheries Society* 101, 627–637.

Bauchot M.L. and Hureau J.C. (1986) Sparidae. In Whitehead P.J.P., Bauchot M.L., Hureau J.C., Nielsen J. and Tortonese E. (eds) *Fishes of the north-eastern Atlantic and the Mediterranean, Volume II.* Paris: UNESCO, pp. 883–907.

Bellido J.M., Pierce G.J., Romero J.L. and Millán M. (2000) Use of frequency analysis methods to estimate growth of anchovy (*Engraulis encrasicolus* L. 1758) in the Gulf of Cadiz (SW Spain). *Fisheries Research* 48, 107–115.

Casselman J.M. (1987) Determination of age and growth. In Weatherley A.H. and Gill H.S. (eds) *The biology of fish growth.* New York: Academic Press, pp. 209–242.

Coelho R., Bentes L., Correia C., Gonçalves J.M.S., Lino P.G., Monteiro P., Ribeiro J. and Erzini K. (2005) Age, growth and reproduction of the axillary seabream, *Pagellus acarne* (Risso, 1827), from the south coast of Portugal. *Thalassas* 21, 79–84.

Erzini K., Bentes L., Coelho R., Correia C., Lino P.G., Monteiro P., Ribeiro J. and Gonçalves J.M.S. (2001) *Fisheries biology and assessment of demersal species (Sparidae) from the South of Portugal.* Commission of the European Communities DG XIV/C/1, Final Report. Ref. 98/082, 263 pp.

FAO Fishery Committee for the Eastern Central Atlantic (2006) *Report of the FAO/CECAF Working Group on the Assessment of Demersal Resources. Conakry, Guinea, 19–29 September 2003.* CECAF/ECAF Series/COPACE/PACE Séries. No. 06/67. Rome, FAO, 357 pp.

FAO Fishery Committee for the Eastern Central Atlantic (2006) *CECAF Working Group on the Assessment of Demersal Resources–Subgroup North. Saly, Senegal, 14–23 September 2004.* CECAF/ECAF Series/COPACE/PACE Séries. No. 06/68. Rome, FAO, 219 pp.

Fischer W., Schneider M. and Bauchot M.L. (1987) *Fiches FAO d'identification des espèces pour les besoins de la pêche. Mediterranée et Mer Noire (zone de peche 37).* Rome: FAO.

Gayanillo F.C., Sparre P. and Pauly D. (1993) *The FISAT user's guide. FAO–ICLARM Stock assessment tools.* Rome: FAO Computerized Information Series/Fisheries, 99 pp.

Gil de Sola L. (1993) Las Pesquerías Demersales del Mar de Alborán (Surmediterráneo Ibérico). Evolución en los últimos decenios. *Informes Técnicos del Instituto Español de Oceanografía* 142, 1–179.

Gunderson D.R. (1977) Population biology of Pacific Ocean perch, *Sebastes alutus*, stocks in the Washington–Queen Charlotte Sound region, and their response to fishing. *Fishery Bulletin* 75, 369–403.

Gutiérrez M. (1967) Coloración histológica para ovarios de peces, crustáceos y moluscos. *Investigación Pesquera* 31, 265–271.

Greco S., Genovese L. and Micale V. (1995) Growth, gonadal histology and liver lipid composition in *Pagellus acarne. Cahiers Options Méditerranéennes* 16, 89–102.

Hunter J.R., Macewicz B.J., Lo N.C.H. and Kimbrell C.A. (1992) Fecundity, spawning, and maturity of female Dover sole *Microstomus pacificus*, with an evaluation of assumptions and precision. *Fishery Bulletin* 90, 101–128.

Krug H.M. (1990) The Azorean blackspot seabream, *Pagellus bogaraveo* (Brünnich, 1768) (Teleostei: Sparidae): reproductive cycle, hermaphroditism, maturity and fecundity. *Cybium* 14, 151–159.

Krug H.M. (1998) Variation in the reproductive cycle of the blackspot seabream, *Pagellus bogaraveo* (Brünnich, 1768) in the Azores. *Arquipélago. Life and Marine Sciences* 16 A, 37–47.

Lamrini A. (1986) Sexualité de *Pagellus acane* (Risso, 1826) (Teleosteen Sparidae) de la côte Atlantique Meridionale du Maroc (21° − 26°). *Cybium* 10, 3–14.

Larrañeta M.G. (1964) Sobre la biología de *Pagellus erythrinus* (L.) especialmente del de las costa de Castellón. *Investigación Pesquera* 27, 121–146.

Le-trong P. and Kompowsky A. (1972) The bronze bream *Pagellus acarne* (Risso) from North-West African region. *Acta Ichthyologica et Piscatoria* 2, 20–30.

Mandich A., Massari A., Bottero S. and Marino G. (2002) Histological and histochemical study of female germ cell development in the dusky grouper *Epinephelus marginatus* (Lowe, 1834). *European Journal of Histochemistry* 46, 87–100.

Mennes F. (1985) Multispecies assessment of fish stocks off the Western Sahara region with emphasis on the family Sparidae. *Naga* 3, 5–10.

Micale V., Maricchiolo G. and Genovese L. (2002) The reproductive biology of blackspot sea bream *Pagellus bogaraveo* in captivity. I. Gonadal development, maturation and hermaphroditism. *Journal of Applied Ichthyology* 18, 172–176.

Morato T., Solà E., Grós M.P. and Menezes G. (2001) Feeding habits of two congener species of seabreams, *Pagellus bogaraveo* and *Pagellus acarne*, off the Azores (Northeastern Atlantic) during spring of 1996 and 1997. *Bulletin of Marine Science* 69, 1073–1087.

Munro J.L. and Pauly D. (1983) A simple method for comparing the growth of fishes and invertebrates. *Fishbyte* 1, 5–6.

Pajuelo J.M. and Lorenzo J.M. (1994) Parámetros biológicos del besugo *Pagellus acarne* (Pisces: Sparidae) en Gran Canaria (islas Canarias). *Boletín del Instituto Español de Oceanografía* 10, 155–164.

Pajuelo J.G. and Lorenzo J.M. (2000) Reproduction, age, growth and mortality of axillary seabream, *Pagellus acarne* (Sparidae), from the Canarian archipelago. *Journal of Applied Ichthyology* 16, 41–47.

Santos M.N., Monteiro C.C. and Erzini K. (1995) Aspects of the biology and gillnet selectivity of the axillary seabream (*Pagellus acarne*, Risso) and common Pandora (*Pagellus erythrinus*, Linnaeus) from the Algarve (south Portugal). *Fisheries Research* 23, 223–236.

Spedicato M.T., Greco S., Sophronidis K., Lembo G., Giordano D. and Argyri A. (2002) Geographical distribution, abundance and some population characteristics of the species of the genus *Pagellus* (Osteichthyes: Perciformes) in different areas of the Mediterranean. *Scientia Marina* 66 (Supplement 2), 65–82.

Shapiro D.Y. (1984) Sex reversal and sociodemographic processes in coral reef fishes. In Potts G.W. and Wooton R.J. (eds) *Fish reproduction: strategies and tactics*. London: Academic Press Inc, 410 pp.

Sokal R.R. and Rohlf F.J. (1995) *Biometry. The principles and practice of statistics in biological research*. San Francisco: W.H. Freeman.

Weibel E.R. (1979) *Stereological methods. Volume 1: Practical methods for biological morphometry*. London, New York and Toronto: Academic Press.

and

Wootton R.J. (1990) *Ecology of teleost fishes*. London: Chapman & Hall.

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