

## Life history of the red-banded seabream *Pagrus auriga* (Sparidae) from the coasts of the Canarian archipelago

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### Summary

Red-banded seabream *Pagrus auriga* (N = 615) were caught off the Canary Islands from January 2003 to December 2004. Total length ranged from 120 to 780 mm. The species was characterized by protogynous hermaphroditism. The male : female ratio was in favour of females (1 : 8.2). The reproductive season extended from September to February, with a peak in spawning activity in October–November. Fifty percentage maturity was reached at 387 mm total length by females and 533 mm by males. The length–weight relationship for all individuals was described by the parameters:  $a = 0.0086$  and  $b = 3.014$ , when length is given in mm and weight in grams. Otolith age readings indicated that the population consists of 19 age groups, including a very high proportion of individuals between 0 and 7 years old. Growth analysis reveals that the species is slow-growing and relatively long lived (18 years). The von Bertalanffy growth parameters for the entire population were:  $L_{\infty} = 803$  mm,  $k = 0.081 \text{ year}^{-1}$  and  $t_0 = -2.17$  year. Growth differed between males and females. The instantaneous rate of natural mortality for all fish was:  $M = 0.164 \text{ year}^{-1}$ .

### Introduction

In the Canarian archipelago (central-east Atlantic), the family Sparidae is represented by 10 genera, one of which is the genus *Pagrus* Cuvier, 1816. This genus is represented by five species distributed around the world; only two species are found in this area: the red-banded seabream *P. auriga* Valenciennes, 1843 and the red porgy *P. pagrus* (Linnaeus, 1758).

*Pagrus auriga* is a demersal marine fish inhabiting various types of sea bottom, especially rocky bottoms. It can be found to depths of about 170 m, but is more abundant in the surf zone. This species is distributed along the Eastern Atlantic, from Portugal to Angola, and around the Madeira, Canary and Cape Verde islands as well as in the Mediterranean Sea (Bauchot and Hureau, 1986, 1990).

In the Canary Islands, the red-banded seabream is an important species in small-scale demersal fisheries and in aquaculture and is caught mainly with traps at depths ranging between 10 and 110 m. It is captured throughout the year but with significant seasonal differences in the landings. No limits are currently imposed on its fishery and only minimum size legislation (350 mm) has been implemented.

Information on the biology of the red-banded seabream is very scarce. Only the sexual changes and the sexual structure

of the population off West African waters have been published (Alekseev, 1982, 1983); his study, however, was carried out only on gonads of two specimens (Alekseev, 1982).

The need for an ecologically based management strategy and the paucity of data available on the ecology of *P. auriga* prompted an investigation into aspects of its life history including population structure, sexuality, spawning cycle, maturity, age and growth and mortality. We examined these ecological aspects in order to understand the life cycle strategy of this species and to compare its population aspects with the information available for the other *Pagrus* species.

### Materials and methods

A total of 615 red-banded seabream specimens were obtained by a random method from commercial catches at different Canary Islands fishing ports between January 2003 and December 2004. Fish were caught with traps at depths of 10–110 m.

Analysis of the samples was completed immediately after landings. Total length ( $L_t$ ) was measured to the nearest millimetre, and total weight ( $W_t$ ) to the nearest 0.1 g. The sex and the stage of maturation of all specimens were recorded by macroscopic examination of the gonads and histological examination. Gonads were removed, weighed to the nearest 0.01 g ( $G_w$ ) and examined macroscopically. Stages of maturation were classified macroscopically as immature (I), resting (II), ripe (III), ripe and running (IV), and spent (V; Holden and Raitt, 1975). The classification of oocyte development was based on criteria used by Wallace and Selman (1981), Buxton (1990) and West (1990). Tissues were fixed in formalin and subsequently processed histologically to enable the observation of the process of gonadal development (oogenesis). The gonads were embedded in paraffin, sectioned at 5  $\mu\text{m}$  and stained with Harris haematoxylin and counterstained with eosin. Finally, otoliths (sagittae) were removed, cleaned and stored dry.

The sexual pattern was established taking into account the sex determinations. The overall sex ratio (males : females) and the sex ratios by size intervals (20 mm) were determined considering the number of males and females. Sex ratios were tested statistically for significant deviations from the expected 1 : 1 ratio with a chi-square test ( $\alpha = 0.05$ ). Cyclical changes in the maturation of the gonads were further investigated by monitoring the variation in the gonadosomatic index, which was calculated by expressing gonad mass as a percentage of

eviscerate body mass (Anderson and Gutreuter, 1983), and estimating the temporal evolution in the frequency of the maturity stages. The length at first maturity was determined as the proportion of reproductively active fish in each size class (stages III, IV and V) and by fitting a logistic ogive:  $P = \frac{100}{1 + e^{-r(L_t - L_m)}}$ , where  $P$  is the percentage of fish mature at length  $L_t$ ;  $L_m$  is the length at first maturity; and  $r$  the model parameter (Saila et al., 1988). The function was fitted to data by means of the Marquardt algorithm for non-linear least squares parameter estimation.

Age was determined by interpreting growth rings on the otoliths. **Whole otoliths were immersed fully in water** and read with a compound microscope (10×) using reflected light following standard techniques. Counts of the growth bands were made without knowledge of the size, sex or previous results for the individual. **Counts were made for otoliths of each individual on two separate occasions**, and only coincident readings were accepted. An index of average percent error (IAPE) was used to compare the accuracy of age determinations (Beamish and Fournier, 1981). Ageing was validated by examination of monthly changes in appearance of the edges of the otoliths (Campana, 2001). This method allowed the annual formation of the rings to be determined; once the rings were confirmed to be annual, the age of each fish was determined and assigned to a year-class taking into account the date of capture, the annuli formation period, and the reproductive biology of the species in the area (Morales-Nin, 1987). Thus, 1 November was considered as the birth date. The von Bertalanffy growth curve was fitted to the observed length at age data of the resulting age-length key by means of the Marquardt algorithm for non-linear least squares parameter estimation using the program FISAT (Gayanilo et al., 1996).

The instantaneous rate of natural mortality ( $M$ ) was estimated using different classical methods (Beverton and Holt, 1959; Tanaka, 1960; Taylor, 1960; Rikhter and Efanov, 1976; Pauly, 1980; Hoenig, 1983). To delimit a range of values of this rate that includes its real value, the longevity for each value of the instantaneous rate of natural mortality was estimated using the method of Alagaraja (1984).

## Results

The *P. auriga* gonads were elongated and suspended by a dorsal mesentery in the posterior region of the visceral cavity. In general, both gonadal lobes were equally well developed.

Of the fish examined, 39 were males, 320 females and 15 intersexuals. The sex of the remaining 241 fish could not be determined macroscopically as they were immature with very thin and translucent gonads. Fish ranged in size from 120 to 780 mm, and weighed between 34 and 9285 g. Males ranged from 440 to 781 mm in length and from 928 to 9285 g in weight. Females ranged from 229 to 665 mm in length and from 224 to 4850 g in weight. Intersexuals ranged in size from 280 to 635 mm, weighing from 457 to 5001 g.

The overall ratio of males to females was 1 : 8.2; thus both sexes were not equally represented, so the hypothesis that the sex ratio was 1 : 1 must be rejected ( $\chi^2 = 219.9 > \chi^2_{1,0.05} = 3.84$ ). Females predominated in smaller size intervals, males in larger intervals, and intersexuals were intermediate in size between males and females (Fig. 1). Sex ratios by size intervals had significant departures from the 1 : 1 ratio for most size categories ( $\chi^2 > \chi^2_{1,0.05} = 3.84$ ), except for the middle size groups (490–650 mm). Individuals with both feminine and masculine gonadal tissue were found by macro-

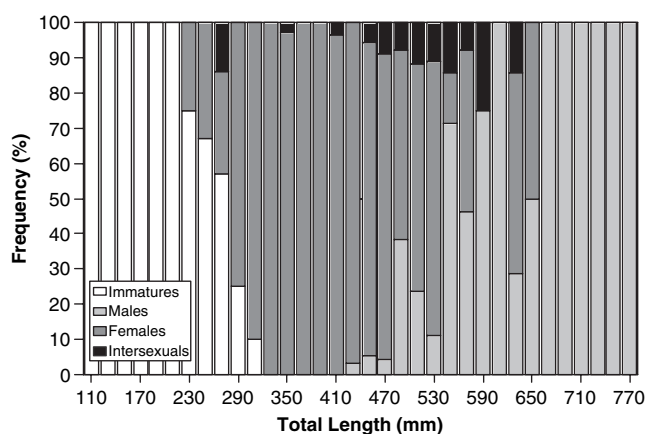


Fig. 1. Size distributions for male, female, intersexual and immature individuals of *Pagrus auriga* off the Canary Islands

scopic observation of the gonads. However, these intersexual individuals accounted for only a small percentage of the total. Intersexual individuals always had one sex more developed than the other. Histological examination of the gonads was developed for validation (Fig. 2).

Males and females with ripe gonads (stage III) were recorded between September and December; ripe and running males and females (stage IV) appeared in October, becoming dominant in November–December; spent males and females (stage V) were recorded mainly from January to February (Fig. 3). The highest values of the gonadosomatic index occurred between September and February, with a maximum in October–November (Fig. 4).

Despite differences in the number of developmental stages recognized in the literature, two major growth phases described by Buxton (1990) were identified in the females: previtellogenesis or cytoplasmatic growth, resulting from oögonia to the end of the perinuclear stage, and vitellogenesis, which included all stages of yolk formation from the primary vesicle oocyte stage to maturation.

The histological description of oögenesis was as follows (Fig. 5): oögonia were characterized by a high nucleus to cytoplasm ratio, small size and lightly basophilic cytoplasm. They were most frequently observed in the peripheral regions of the ovigerous lamellae and predominated after the spawning

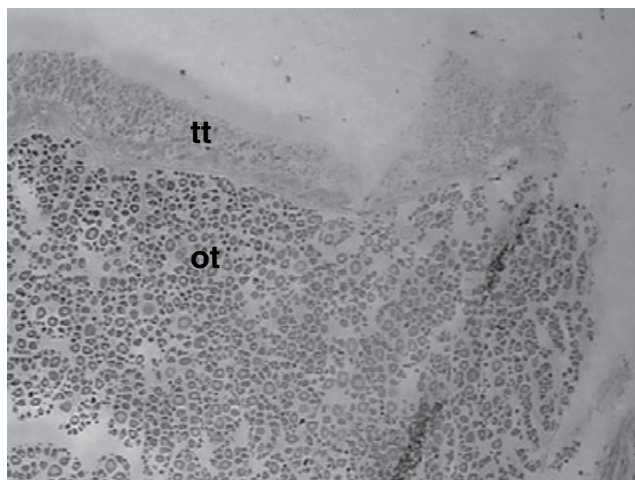


Fig. 2. Transverse sections through intersexual gonads of *Pagrus auriga* off the Canary Islands. tt, testicular tissue; ot, ovarian tissue

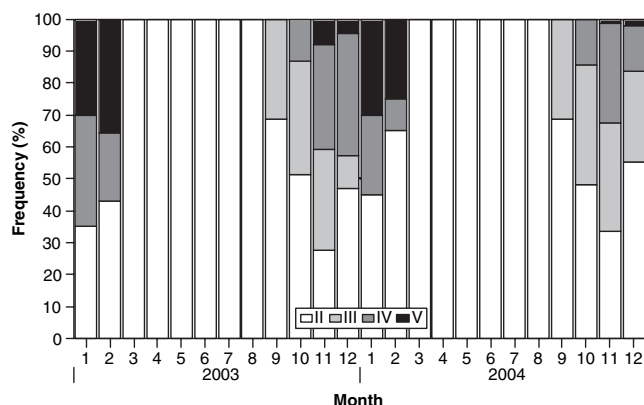


Fig. 3. Mean monthly frequency of maturity stages for combined sexes of *Pagrus auriga* off the Canary Islands. Maturity stages: (II) resting, (III) ripe, (IV) ripe and running, and (V) spent

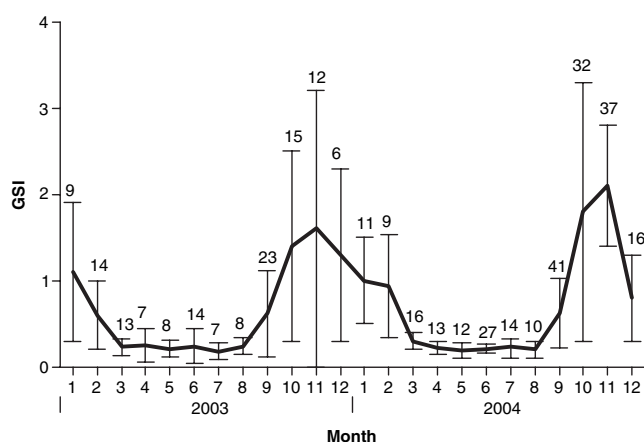


Fig. 4. Monthly development of the gonadosomatic index (GSI) for sexes combined of *Pagrus auriga* off the Canary Islands. Vertical bars indicate standard deviation

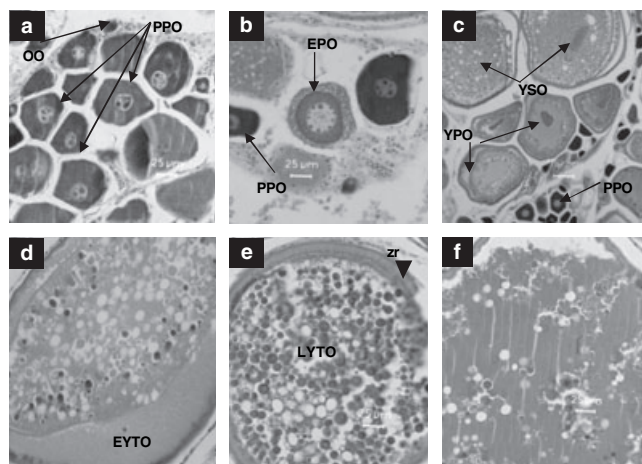


Fig. 5. Transverse sections through female gonads of *Pagrus auriga* off the Canary Islands illustrating oogenesis. (a) Immature ovary containing oögonia (OO) and pre-perinuclear oocytes (PPO). (b) Immature ovary containing early perinuclear oocytes: PPO and early perinuclear oocyte (EPO). (c) Transverse section through a developing ovary showing PPO, primary vesicle stage (YPO) and secondary yolk vesicles oocytes (YSO). (d) Transverse section through a developing ovary showing a yolk granule oocyte. Early yolk granule oocyte (EYTO). (e and f) Late yolk granule oocyte (LYTO). The zone radiate (zr) in the tertiary yolk vesicle stage or yolk granule oocyte

season. With further growth of the oocyte (perinuclear oocytes) there was an increase in the relative volume of cytoplasm, which also became strongly basophilic. Perinuclear oocytes had numerous nucleoli and each cell was surrounded by a theca. Pre-perinuclear oocytes were polygonal in shape with an intensely basophilic cytoplasm. The nucleus contained one or two large nucleoli and numerous small ones. Early and late perinuclear oocytes were larger, more ovoid in shape and were less basophilic, with a proliferation of nucleoli in the nucleus. In late perinuclear oocytes the nucleoplasm has a granular appearance and the nucleoli became flattened against the nuclear membrane.

The formation of the follicular epithelial layer or zone granulose below the theca cells, the appearance of the zone radiate at the oocyte surface between the cytoplasm and the zone granulose, marks the end of the primary growth phase and the beginning of vitellogenesis. This phase was followed by the appearance of primary yolk vesicles (cortical alveoli) in the cytoplasm. Vitellogenesis was initiated by the formation of acidophilic 'secondary' yolk globules, which appeared first in the region of the primary yolk vesicles, but later also as extra vesicular yolk throughout the cytoplasm. Yolk accumulation continued until it obscured the cortical alveoli, entirely filling the cytoplasm in the tertiary yolk vesicle stage. In this stage the zone radiate was clearly visible. Towards the end of development the lipid drop formation displaced the nucleus to the oocyte periphery of cell, followed by a degeneration of the nuclear membrane and the coalescence of yolk. Histological examination of mature eggs was unsatisfactory, with oocytes collapsing during tissue dehydration. Atresia associated with the termination of gonadal recrudescence was characterized by hypertrophy of the follicle granulose and the disintegration of the zone radiate and both nuclear membrane and the nucleus.

Sexual maturity ogives for males and females are shown in Fig. 6. The length at which 50% maturity is reached was 387 mm for females and 533 mm for males. There was a significant difference in the length at 50% maturity between sexes ( $t$ -test,  $t = 0.65 > t_{0.05,32} = 2.02$ ).

The use of *sagittal* otoliths for estimating the age of the red-banded seabream proved straightforward, with distinct opaque and hyaline bands surrounding a white opaque nucleus. Of 308 otoliths processed for annual age estimation, 29 (9.4%) were considered unreadable. Of the remaining 279 otoliths, 256 (91.5%) of the readings coincided at least twice whereas 23 (8.5%) yielded conflicting ages and were excluded from the

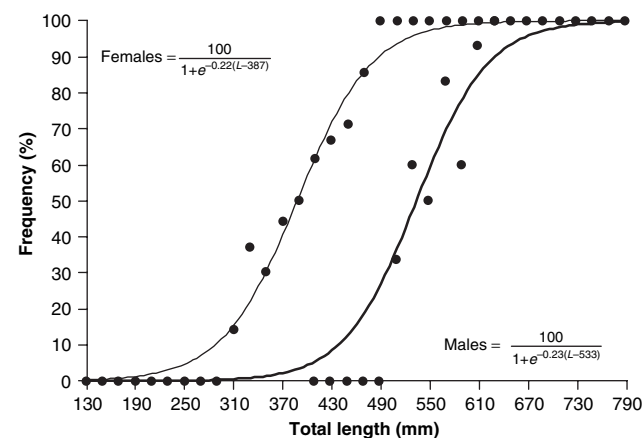


Fig. 6. Sexual maturity ogives for *Pagrus auriga* males and females off the Canary Islands



analysis. The low value of the IAPE (2.83%) indicated high precision in the ageing.

Otoliths showed a seasonal variation in the formation of hyaline and opaque rings. Opaque and hyaline edges were noted in all months, but the general pattern indicated that two rings, one opaque and one hyaline, were deposited during 1 year. The opaque ring was formed between May and October, mainly in July and August, and the hyaline ring was formed during the remaining months (Fig. 7).

Fish aged 0–18 years were found (Table 1). The von Bertalanffy growth curves are shown in Fig. 8. The predicted length at age of males was greater than that of females, and estimates of asymptotic length were higher for males than for females. Significant differences in the growth parameters were found between males and females (Hotelling's  $T^2$ -test;  $T^2 = 98.25 > T^2_{0.05,3,252} = 7.91$ ).

The values of the instantaneous rate of natural mortality in accordance with the longevity values (more than 18 years) ranged between 0.17 and 0.19 years<sup>-1</sup>, with a mean value of

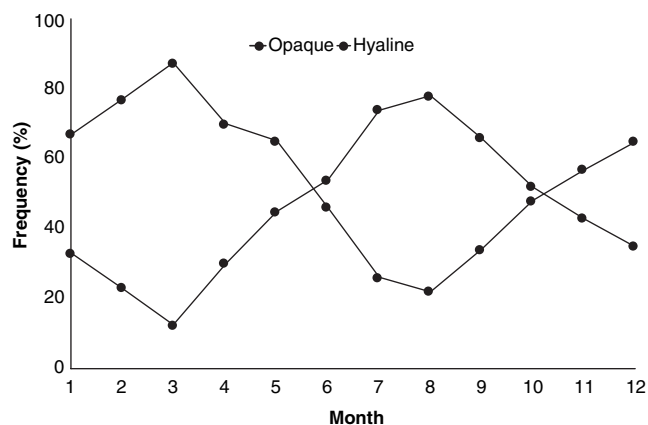


Fig. 7. Monthly percentage of otoliths with opaque and hyaline edge for all *Pagrus auriga* individuals off the Canary Islands

Table 1

Observed mean length at age (mm) and expected mean length at age (mm) according to the von Bertalanffy growth curve for immatures, females and males of *Pagrus auriga* off the Canary Islands (n is the number of fish)

Age (years)	Immatures			Females			Males		
	n	Length observed (mm)	Length expected (mm)	n	Length observed (mm)	Length expected (mm)	n	Length observed (mm)	Length expected (mm)
0	22	172	119						
1	52	182	167						
2	8	204	213	1	240	234			
3	8	248	257	11	311	280			
4	1	280	298	26	342	320			
5				33	368	357			
6				16	391	390			
7				18	394	419			
8				10	437	446			
9				7	456	469	2	510	473
10				7	490	490	1	515	502
11				3	500	509	5	531	530
12				2	552	526	1	552	557
13				3	550	541	2	581	582
14				1	665	555	3	567	605
15							2	577	628
16				1	630	578	1	690	649
18							1	760	688

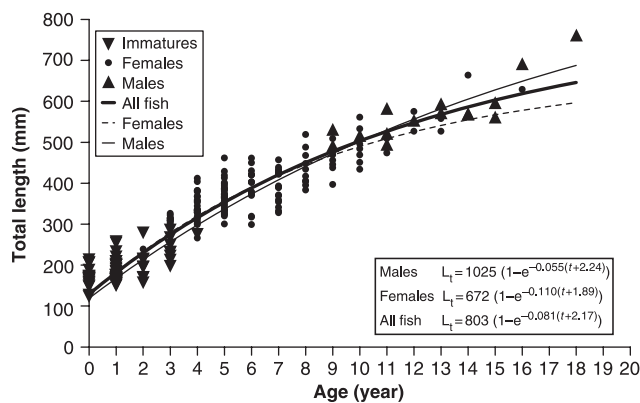


Fig. 8. von Bertalanffy growth curves fitted to data for males, females, as well as all *Pagrus auriga* off the Canary Islands

0.18 years<sup>-1</sup>; the corresponding values of longevity ranged between 24 and 27 years.

## Discussion

Among the numerous families of teleosts, sparids exhibit some of the most diversified expressions of sexuality. In this family, both forms of sequential hermaphroditism (protogynous or protandrous) have been recognized, as well as rudimentary hermaphroditism leading to secondary gonochorism (Buxton and Garratt, 1990). This variability is probably linked to the peculiar configuration of the gonad, an ovotestis, which is characteristic of all species of the family.

The present study confirmed that red-banded seabream off the Canary Islands are hermaphrodite, as was observed for *P. auriga* in West Africa (Aleksiev, 1982, 1983). *Pagrus major* in the Pacific Ocean (Matsuura et al., 1987; Matsuyama et al., 1987, 1988), *P. caeruleostictus* and *P. pagrus* in the Mediterranean Sea (Chakroun and Kartas, 1987; Vassilopoulou and Papaconstantinou, 1992), and *P. caeruleostictus*, *P. africanus* and *P. pagrus* in the Atlantic Ocean (Manooch, 1976;

Alekseev, 1982, 1983; Buxton and Garratt, 1990; Pajuelo and Lorenzo, 1996) also exhibit hermaphroditism. This phenomenon seems to be a characteristic of the genus.

The observation of individuals with well developed ovotestes and bimodal size frequencies distribution, with females occupying the smaller size classes, and the females biased sex ratios suggests the occurrence of protogynous sex changes. However, the presence of non-functional gonadal tissue of one gender in individuals containing functional tissue of the other gender is not sufficient to label a species as hermaphrodite (Sadovy and Shapiro, 1987). In the present study, the fact that fish were encountered possessing ovotestis, both of which were growing in size and developing with well-organized ovigerous lamellae, indicates that they are true transitionals. This characteristic has also been noted for the same species in West Africa (Alekseev, 1982, 1983), for *P. major* in the Pacific Ocean (Buxton and Garratt, 1990), and for *P. caeruleostictus*, *P. africanus* and *P. pagrus* in the Atlantic Ocean (Alekseev, 1982, 1983; Buxton and Garratt, 1990; Pajuelo and Lorenzo, 1996). Protogynous seems to be the common reproductive style in the *Pagrus* genus.

Sex inversion, which is the change from one sex to another in a single individual, is a very common phenomenon in the family Sparidae (Buxton and Garratt, 1990; Micale and Perdicchi, 1994). Sex reversal was accompanied by resorption and restructuring of the ovarian tissue and subsequent resurgence of the spermatogenesis. According to Sadovy and Shapiro (1987), this is the strongest evidence of protogynous. The presence of intersexuals in a wide size range (270–630 mm) suggests that the sex conversion does not occur simultaneously for all males (Alekseev, 1983). The intersexual individuals are mainly comprised of 430–590 mm; thus, sexual succession takes place mainly between 7 and 14 years of life. The scarcity of individuals with both developed ovarian and testicular tissues in the samples indicates a rather brief transitory phase between sexes for each individual. The absence of females in the largest size classes implies that sex conversion is essential for all fish. In this sense, Alekseev (1983) pointed out that *P. auriga* is characterized by obligatory functional protogyny.

The sex structure of the population, with a predominance of females vs males, is mainly determined by the nature of the sexual change. Related to this, Smale (1988) indicated that sex ratios of protogynous sparids might be skewed towards the females. A predominance of females has also been noted for the same species in West Africa (Alekseev, 1982, 1983), for *P. pagrus*, in the Atlantic Ocean (Cotrina and Cousseau, 1975; Manooch, 1976; Manooch and Hassler, 1978; Alekseev, 1982, 1983; Lozano et al., 1990; Pajuelo and Lorenzo, 1996) and in the eastern Mediterranean (Vassilopoulou and Papaconstantinou, 1992), and for *P. africanus* and *P. caeruleostictus* on the African coast (Alekseev, 1982, 1983).

In the Canarian archipelago, the reproductive season of the red-banded seabream extends from September to February, with maximal gonadal activity in November–December. The protracted spawning season recorded in this study indicates a protracted period of favourable environmental conditions for hatching and larval development. An extensive spawning period has also been found for *P. caeruleostictus* (Giret, 1974) and for *P. pagrus* (Ciechomski and Weiss, 1973; Manooch, 1976; Manooch and Hassler, 1978; Vassilopoulou and Papaconstantinou, 1992; Pajuelo and Lorenzo, 1996).

The seasonal development of the gonadosomatic index confirms spawning in the winter, as found mainly for other *Pagrus* species such as *P. pagrus* and *P. caeruleostictus*

(Manooch, 1976; Manooch and Hassler, 1978; Kromer, 1994; Pajuelo and Lorenzo, 1996). The values of the gonadosomatic index achieved at spawning are very similar to those observed for moderately fecund sparids such as *P. pagrus* (Manooch and Hassler, 1978; Pajuelo and Lorenzo, 1996) and higher than those observed for relatively low fecund sparids such as *Chrysoblephus puniceus* and *Cheimereus nufar* (Garratt, 1985).

Age at maturity is 5 years for females and 11 years for males. Differences in length and age at sexual maturity between males and females found in the present study can be adequately explained by the sexual change. Shorter length at maturity for females than for males has also been obtained for *P. pagrus* in the Canary Islands (Pajuelo and Lorenzo, 1996), in North Carolina (Manooch, 1976; Manooch et al., 1981) and in the eastern Mediterranean (Vassilopoulou and Papaconstantinou, 1992).

The oldest age estimate obtained in this study is 18 years and the phenomenon of stacking is not evident. The maximum age observed for *P. auriga* compares well with values reported for *P. pagrus* in the Argentine Sea (Cotrina and Cousseau, 1975), in North Carolina (Manooch, 1976) and in the Canary Islands (Pajuelo and Lorenzo, 1996).

The high percentage of otoliths with hyaline edge observed during the winter months could be related to physiological stress during the spawning of the species. Nevertheless, because these rings are present in juveniles as well as adults, they should also be related to the lowest values of sea temperature (18°C). The high percentage of otoliths with an opaque ring on the edge during summer, attributed to a fast growth period, could be due to temporal variation in food resources (more abundance) and the high sea temperature (24°C). The evidence currently available suggests that a seasonal temperature difference of 6°C might be sufficient to cause ring formation (Morales-Nin and Ralston, 1990). Similar findings have been recorded in other studies carried out in the Canarian archipelago on other sparid species such as *P. pagrus*, *Spondyllosoma cantharus*, *Pagellus acarne*, *Diplodus sargus* and *D. cervinus* (Pajuelo and Lorenzo, 1996, 1999, 2000, 2002, 2003).

The difference in growth between sexes, with males slightly longer than females at the same age, is a characteristic of the protogynous species such as the red-banded seabream. Alekseev (1983) pointed out that the mean size of sex reversed fish is slightly larger than same-age females; therefore, the difference in size between males and females of the same age cannot be considered as evidence of an intersexual difference in growth rates because males and females are the same specimens at different stages of sexual succession and, possibly, the largest females in an age group are the first to revert.

Some of the values obtained for the instantaneous rate of natural mortality are unrealistic because the life spans expected using only these data are lower than the maximum age observed for the population under a natural and fishing mortality. The estimated range of values of *M* obtained is very similar to that reported for other sparids off the Canary Islands with similar life history characteristics such as *Dentex gibbosus*, *P. pagrus* and *D. sargus* (Pajuelo and Lorenzo, 1995, 1996, 2004).

To understand where the *P. auriga* species fits into this life history classification continuum, various life history parameters such as maximum length, maximum age, growth rate and size and age at maturity, must be analysed together (Buxton and Clarke, 1991). In this context, the life history parameters

of the red-banded seabream suggest that this species has a specialized life history style. Fisheries based on *k*-selected species are more susceptible to growth overfishing and stock depletion (Buxton and Clarke, 1991; Booth and Buxton, 1997). Slow growth might result in a lower yield per unit stock, because of a lower production/biomass ratio and a slower recovery rate after overexploitation. Red-banded seabream has also medium-size ovaries in large individuals during the spawning season, suggesting that it is moderately fecund and that a moderate number of eggs are released during the spawning season. As a result, it may be more sensitive to heavy exploitation than species exhibiting a higher reproductive output (Smale, 1988). As a consequence, the life history characteristics of this species make the stock more prone to overexploitation due to a rapid reduction in surplus production (Booth and Buxton, 1997).

In the Canary Islands, a minimum size limit has been implemented for the target species. In the case of the red-banded seabream, the minimum size regulation is of limited benefit because the minimum length, which may be legally kept, is smaller than the length at first maturity. The practical problem is that this species is only one component of the exploited multispecies demersal fish community and matures at a different size than the other species caught jointly; therefore, it is susceptible to exploitation at a size when many other coexisting demersal species are mature or immature. Release of these fishes once captured is of dubious benefit as they often suffer from barotrauma when brought to the surface from more than 30 m and will often not survive when released (Smale, 1988).

Another protection strategy has been introduced with the building of artificial reefs. This protection appears to cover only the earlier stages of the life cycle and encompasses only limited areas. When immature individuals move out of artificial reefs, they are subject to a high exploitation level because fishermen deploy a large number of traps around the reef. Finally, measures such as closed seasons or changes in fishing patterns are desirable to safeguard the spawning stock and the recruits, especially if the stock continues to decline.

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