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The reproductive biology of the grey triggerfish *Balistes capriscus* (Pisces: Balistidae) in the Gulf of Gabès (south-eastern Mediterranean Sea)

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Fundamental information on the reproductive biology of the grey triggerfish Balistes capriscus *from the Gulf of Gabès (south-eastern Mediterranean Sea) is based on 751 specimens, collected between June 2005 and May 2010, from commercial catches at different fishing ports at Chebba (34°14′N 11°06′E), Kerkennah (34°45′N 11°17′E) and Zarzis (33°41′N 11°48′E). The species were caught in this area using pelagic trawl nets. The calculation of the gonadosomatic index suggested that the spawning season of grey triggerfish occurred mainly between July and mid-September with a peak in July, coinciding with summer time. The first maturation occurred at 20.26 cm fork length for females and 21.3 cm fork length for males. The monthly values of hepatosomatic index and condition factor (K) indicated that the liver was the most severely stressed organ in the reproduction process of energy transfer. The absolute fecundity (F) ranged from 290,120 to 984,990 eggs per female. The fecundity of the species was determined by the size and weight of the individuals.*

Keywords: *Balistes capriscus*, first maturity, fecundity, Gulf of Gabès, Tunisia

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INTRODUCTION

The grey triggerfish, *Balistes capriscus* Gmelin, 1789, is an amphi-atlantic fish widely found in the eastern Atlantic from the British Isles to Angola, including the Mediterranean Sea (Harmelin-Vivien & Quero, 1990) and the western Atlantic from the Gulf of Mexico to Argentina (Robins & Ray, 1986). This fish represents an important member of reef fish assemblages and is commonly associated with coral reefs, wrecks, outcroppings, artificial structure and hard bottom areas (Frazer & Lindberg, 1994; Wilson *et al.*, 1995; Stanley & Wilson, 2003; Gledhill, 2005; Lingo & Szedlmayer, 2006).

Over the last decade, the expansion of this fish has progressed in its northern range probably due to the global warming effects (Francour *et al.*, 1994; Astraldi *et al.*, 1995; Garrabou *et al.*, 2003). Recently, a considerable increase of *B. capriscus* production occurred along the Tunisian coast and particularly in the Gulf of Gabès from 34 tons in 1990 to 187 tons in 2009 (FAO, 2011).

The increase of production, as well as the high commercial value of the grey triggerfish, due to its appreciation by local consumers, has led to an experimental study of the reproduction biology in order to allow a sustainable exploitation of this fish.

Previous studies on the reproductive biology have been focused on determining the spawning season and size at sexual maturity of *B. capriscus*. They have focused on certain distribution areas: western Atlantic (Dooley, 1972; Wilson *et al.*, 1995; Ingram, 2001; Moore, 2001; Bernardes, 2002; MacKichan & Szedlmayer, 2007), eastern Atlantic (Caverivière *et al.*, 1981; Manooch, 1984; Ofori-Danson, 1990) and north-eastern Mediterranean (İşmen *et al.*, 2004). However, no study has been reported on the annual reproductive cycle and fecundity of *B. capriscus* collected from the south-eastern Mediterranean Sea.

The aim of this work is to provide further information on the reproductive biology. Some parameters such as sexual cycle, spawning period, hepatic and muscular energy reserve changes, as well as the length at the first sexual maturity were analysed to compare ours results with those available in the literature.

MATERIALS AND METHODS

A total of 751 specimens of *B. capriscus* were analysed between June 2005 and May 2010. The samples were collected from commercial catches at different Tunisian fishing ports: Chebba (34°14′N 11°06′E); Kerkennah (34°45′N 11°17′E); and Zarzis (33°41′N 11°48′E). The species were caught in this area using pelagic trawl nets. In the laboratory, the following data were recorded for all individuals: sex, total length (TL), fork length (FL) and standard length (SL) to the nearest mm; total weights (TW) and eviscerated fish weights (EW) to the nearest 0.1 g and the weights of gonads (GW) and livers (LW) were recorded to the nearest 0.01 g.

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Sex-ratios (number of females/number of males) were calculated according to the size, month and season and were compared by applying the χ^2 test.

The reproductive period was determined by analysing the monthly changes in the gonadosomatic index (GSI). The latter was given by the formula:

$$\text{GSI}(\%) = (\text{weight of gonads/weight of eviscerated body}) \times 100.$$

It was calculated for each fish and all values were averaged monthly. The monthly variations in the GSI indicate the evolution in gonad weight during the year and enable description of the various stages of the sexual cycle. Correlation between GSI and temperature was tested using the Spearman rank correlation coefficient (rs) (Zar, 1999).

Seawater average temperature data were supplied by the National Institute of Meteorology in Tunisia.

Organs capable of accumulating and depleting resources for *B. capriscus* in the Gulf of Gabès were determined after analysing the monthly changes of the hepatosomatic index (HSI) and the condition coefficient (K). These parameters were calculated as follows:

$$\text{HSI} = (\text{LW/EW}) \times 100 \text{ (Fouda } et\ al.\text{, 1993);}$$

$$K = (\text{EW/FL}^3) \times 100;$$

where LW = liver weight (g); EW = eviscerated weight (g) and FL= fork length (cm).

Variations in the mean of these indices during the reproductive period were tested using one-way analysis of variance (ANOVA). The *post-hoc* Tukey's test was performed to determine the pair-wise differences.

In order to estimate the size at first sexual maturity (L_{50}), the proportion (Pi) of mature individuals by sex and size-class was calculated:

$$\text{Pi} = (M_i/I_{ei}) \times 100,$$

where M_i represents the number of mature individuals in the size I, and I_{ei} is the number of examined individuals for the same size-class, i.

The obtained data were fitted to a logistical function using the software 'FSAS' (Saul *et al.*, 1988). This function has the advantage of providing a precise estimation of the L_{50} lengths that are often required by most software to analyse the fish stocks.

The equation used to determine the L_{50} was:

$$P = \frac{1}{\left(1 + e^{-r(L-L_{50})}\right)} \text{ (Pauly, 1980)}$$

where P: the proportion of mature individuals; L: the fork length corresponding to the proportion (P); r: constant and L_{50}: the mean size at first sexual maturity; it was taken as the size at which 50% of individuals were mature.

Fecundity was estimated as the total count of mature oocytes in both ovaries from 39 sampled females ranging from 23.2 to 36.1 cm FL fixed in formalin, caught between June and August. Absolute fecundity was determined by the counting–weighing method, the number of eggs in 0.01 g being counted (Kucheryavyi *et al.*, 2007). It was determined according to the following formula:

$$N = nW/w$$

where N and n are the total and partial number of eggs, respectively, and W and w the total and partial weight of eggs, respectively (Yamazaki *et al.*, 2001). Absolute fecundity was recorded as the number of yoked oocytes in the ovaries of the sample. Relative fecundity (number of yoked oocytes per weight), was calculated for TW, EW and GW for each specimen.

Oocytes diameter was determined using a Leica stereomicroscope at magnification 2 × (every magnification had a calibrated millimetre scale). The relationship between absolute fecundity and FL, EW and GW was estimated.

RESULTS

Macroscopic observation on the gonads of *Balistes capriscus*, followed by a squatch for juveniles, was made to distinguish males from females. Furthermore, sexual dichromatism was observed. We can distinguish females from males by the skin colour at the upper side. The former have a white colour, while the latter shows a purplish to bluish reflection. This dichromatism is more pronounced and more accentuated during the reproduction period. No case of hermaphrodism was found and, consequently, *B. capriscus* is a gonochoric fish.

According to this study, 480 females and 276 males, out of 756 identified specimens, were found. An overall sex-ratio of (1:1.74) was significantly in favour of females (χ^2, $P < 0.05$) (Table 1). When grouping individuals by size of 2 cm, we found that for small size-classes, the sex-ratio was balanced. However, beyond 14 cm, FL females were significantly higher and the sex-ratio showed variability with size ($\chi^2 = 91.49$, df = 14, $\alpha = 0.05$).

Table 1. Variation of the proportion of females, males and sex-ratio of *Balistes capriscus* in the Gulf of Gabès according to size (bold numbers indicate significant effects).

FL (cm)	NM	NF	%M	%F	Sex-ratio	χ^2
[10–12]	5	4	56	44	0.80	0.11
[12–14]	14	19	42	58	1.36	0.76
[14–16]	3	13	19	81	4.33	**6.25**
[16–18]	15	29	34	66	1.93	**4.45**
[18–20]	18	34	35	65	1.89	**4.92**
[20–22]	29	47	38	62	1.62	**4.26**
[22–24]	18	33	35	65	1.83	**4.41**
[24–26]	33	53	38	62	1.61	**4.65**
[26–28]	23	39	37	63	1.70	**4.13**
[28–30]	18	32	36	64	1.78	**3.92**
[30–32]	23	41	36	64	1.78	**5.06**
[32–34]	16	30	35	65	1.88	**4.26**
[34–36]	25	41	38	62	1.64	**3.88**
[36–38]	29	47	38	62	1.62	**4.26**
>38	7	18	28	72	2.57	**4.84**

FL, fork length; NM, number of males; NF, number of females; %M, percentage of males; %F, percentage of females.

Table 2. Monthly variation of the proportion of females, males and sex ratio of *Balistes capriscus* in the Gulf of Gabès. Bold numbers indicate significant effects.

Month	NM	NF	%M	%F	Sex-ratio	χ^2
D	18	23	44	56	1.28	0.61
J	5	8	38	62	1.60	0.69
F	17	19	47	53	1.12	0.11
Winter	40	50	44	56	1.25	1.11
M	23	39	37	63	1.70	**4.13**
A	15	29	34	66	1.93	**4.45**
M	18	47	28	72	2.61	**12.94**
Spring	56	115	33	67	2.05	**20.36**
J	32	67	32	68	2.09	**12.37**
JT	41	63	39	61	1.54	**4.65**
A	43	69	38	62	1.60	**6.04**
Summer	116	199	37	63	1.72	**21.87**
S	23	41	36	64	1.78	**5.06**
O	18	34	35	65	1.89	**4.92**
N	23	41	36	64	1.78	**5.06**
Autumn	64	116	36	64	1.81	**15.02**

FL, fork length; NM, number of males; NF, number of females; %M, percentage of males; %F, percentage of females.

Seasonal variations in the sex-ratio of *B. capriscus* showed an apparent dominance of females compared to males (Table 2), but this difference was not significant from December to February (χ^2, $P > 0.05$).

The curves of the GSI monthly values were unimodal for both males and females (Figure 1). Thus, the *B. capriscus* is reproduced once a year. The GSI increases with the progressive rise of the gonads in both sexes until reaching maturity. Then, the index declines sharply in the spawning period.

The high values of GSI were depicted between June and August showing a peak in July. The index values for July were significantly higher for females ($F = 15{,}632$; df (11,479); $P < 0.001$) and males ($F = 2{,}056.36$; df (11,275); $P < 0.001$).

Significant correlations were obtained between the average GSI values of both sexes (females and males) and sea surface temperature ($r_s = 0.582$; $n = 12$; $P < 0.05$ for females) ($r_s = 0.628$; $n = 12$; $P < 0.05$ for males) (Figure 2). Based on these correlations, we note that the complete gonad maturity occurs at the highest sea surface temperature (27°C).

The hepatosomatic index (HSI) of females (8.92 ± 2.01) and males (9.05 ± 1.75) was not significantly different (Mann–Whitney U-test, $Z = -0.89$, $P > 0.05$). HSI of both sexes showed a clear seasonal pattern, evidencing a significant variation across months (females: H Kruskal–Wallis = 161.13, $P < 0.001$; males: H Kruskal–Wallis = 162.37, $P < 0.001$).

The HSI cyclic evolution for both sexes was slightly synchronous with that of GSI showing a peak in June (female HSI: 11.89 ± 0.62 and male HSI: 11.65 ± 0.18), while the condition factor K shows no fluctuation along the year (Figure 3).

The changes in the proportion of the mature individuals showed that below 16 cm size, no individual whatever its sex was mature. The smallest females and males were mature at size 18.9 and 20.5 cm, respectively.

The logistic curves describing the relationship between the maturity proportion in each length interval and the fork length were estimated. The results obtained by the application of the logistical function showed that the size at first sexual maturity was 20.26 cm for females and 21.30 cm for males (Figure 4). The χ^2 test did not show any significant differences between the theoretical proportions and the observed ones and this non-linear logistic regression model had an excellent fit ($r^2 = 0.98$).

Absolute fecundity increased with size: a maximum value of 984,990 oocytes for a size of 36.1 cm and a minimum value of 290,120 oocytes for a size of 23.2 cm, with a mean value of 616,289.512 ± 196,914.792. Based on the latter, the

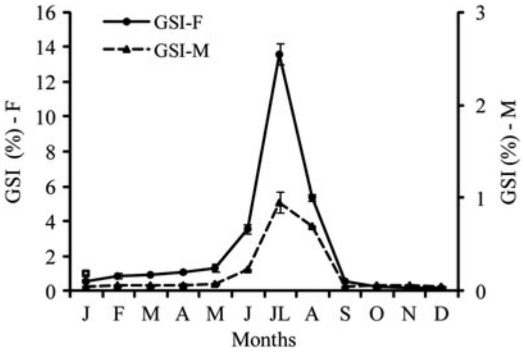

Fig. 1. Monthly gonadosomatic index (GSI), mean values (±standard deviation) for both sexes of grey triggerfish *Balistes capriscus* in the Gulf of Gabès. GSI-F, female GSI; GSI-M, male GSI.

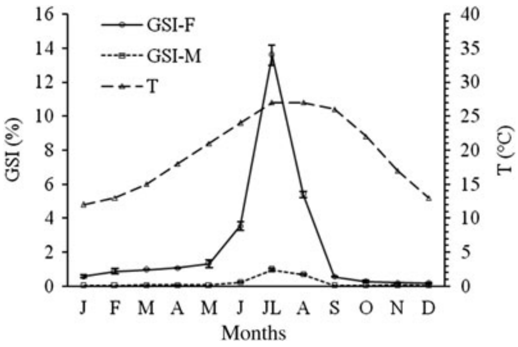

Fig. 2. Monthly gonadosomatic index (GSI), mean values (±standard deviation) for both sexes of grey triggerfish *Balistes capriscus* and of the mean temperature of seawater (T°C) in the Gulf of Gabès (temperature data were supplied by the National Institute of Meteorology). GSI-F, female GSI; GSI-M, male GSI; T, mean temperature of seawater (°C).

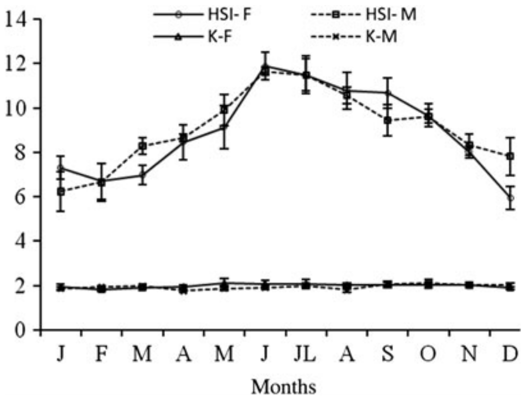

Fig. 3. Monthly hepatosomatic index (HIS) and condition factor, *K*, mean values (±standard deviation) for both sexes of grey triggerfish *Balistes capriscus* in the Gulf of Gabès. HSI-F, female HSI; HSI-M, male HSI; K-F, female condition factor; K-F, male condition factor.

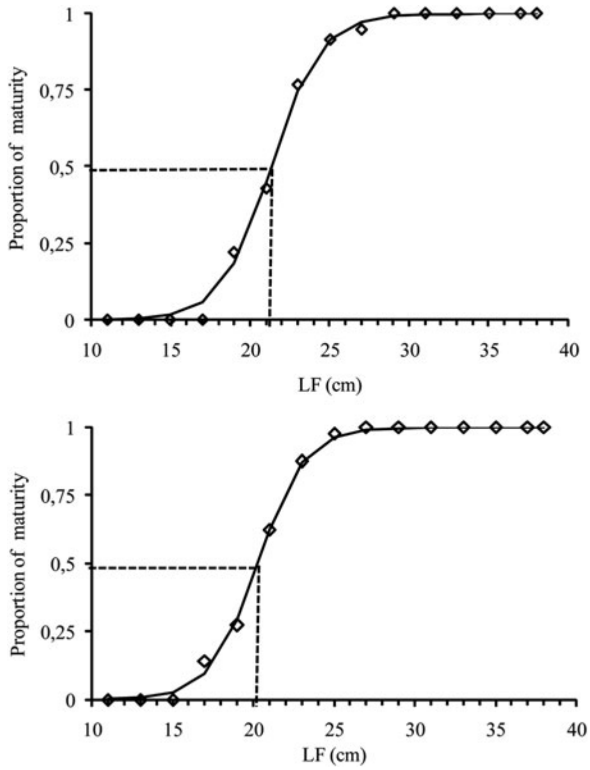

Fig. 4. Size at first sexual maturity of *Balistes capriscus* in the Gulf of Gabès

estimated absolute fecundity is the annual fecundity. Fecundity (F) increased with TL, EW and GW. The relationships between absolute F and FL, EW and GW are described in Figure 5. Fecundity relative to TW, EW and GW is summarized in Table 3.

DISCUSSION

Sexual dichromatism concerning the colour of the upper side was already observed in *B. capriscus*, collected from off the Gulf of Gabès. This character has been described by several authors in other sites. Garnaud (1960) proved that during the period of reproduction, the male has more pronounced colour. Gerlotto & Stéquert (1981) reported that *B. capriscus* has a sexual dichromatism in which males and females were different in skin colour at the sub-opercular region. Mackichan & Szedlmayer (2007) showed that the dominant males could be identified by coloration and behaviour.

The intensity and melanic colours are commonly regulated within few seconds through melonocyte-stimulating hormone, which induces the stimulation of melanin granule dispersion in the melanocytes (Metz *et al*., 2006). Variation in melanic coloration can be genetically determined, and also be influenced by the environment, such as temperature and light (reviewed in Price *et al*., 2008). Furthermore, sexual dimorphism in the length and weight has also been observed for this species in the Gulf of Gabès. In fact, males were significantly larger than females. Similar results have been reported from other areas (Ingram, 2001; Moore, 2001; MacKichan, 2008).

In the Gulf of Gabès, the sex-ratio of *B. capriscus* is generally favourable to females. It is also the case in the north-eastern Gulf of Mexico (Mackichan & Szedlmayer, 2007; Simmons & Szedlmayer, 2012). Only the populations of Alexandretta (southern Turkey) have a male-dominated ratio (İşmen *et al*., 2004). The imbalance of the sex can be

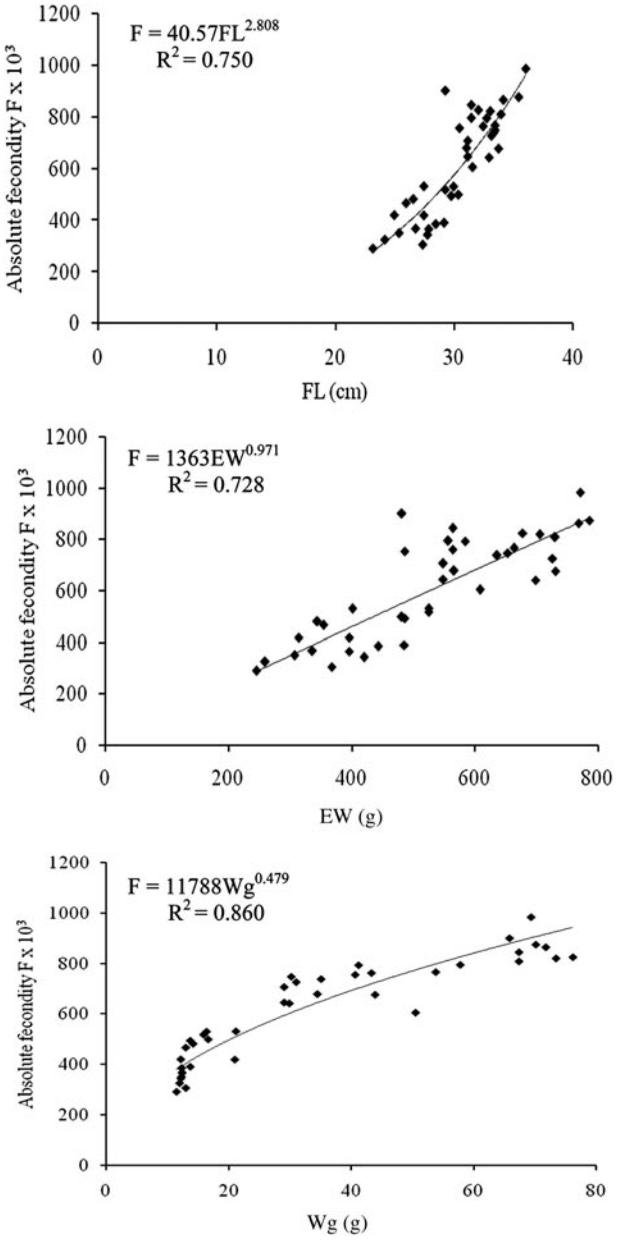

Fig. 5. Relationship between absolute fecundity (F) and fork length (FL), eviscerated weight (EW) and gonad weight (GW) of *Balistes capriscus* in the Gulf of Gabès.

Table 3. Fecundity relative to total weight, eviscerated weight and gonads weight of *Balistes capriscus* in the Gulf of Gabès.

	Min	Max	Mean	SD (±)
N/WT(g)	692.102	1451.818	997.300	176.48
N/EW(g)	803.010	1870.142	1159.523	219.84
N/GW(g)	10,836.702	36,198.092	22,544.453	7,944.96

Min, minimum; Max, maximum; SD, standard deviation; N, number of yoked oocytes; TW, total weight; EW, eviscerated weight; GW, gonad weight.

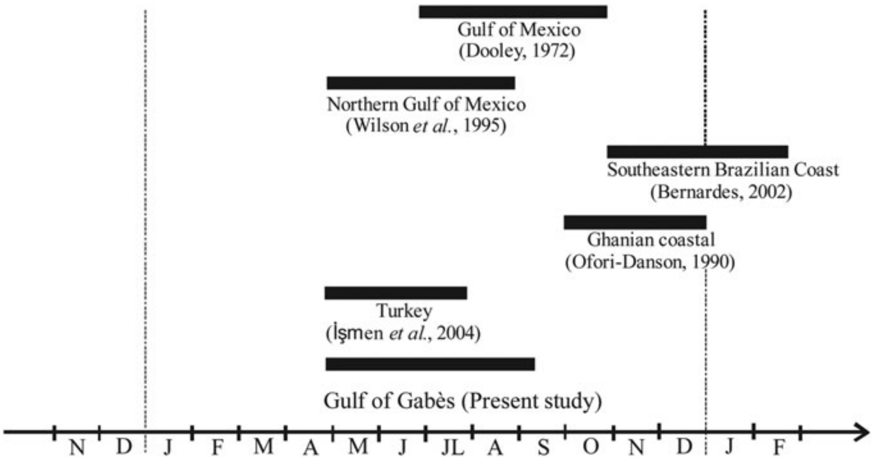

Fig. 6. Reproduction period of *Balistes capriscus* in different regions of the world.

attributed to longevity, a differential catchability of the sexes or a spatio-temporal segregation of the sexes (Morato *et al.*, 2003). In the Gulf of Gabès, female dominance is probably related to a spatio-temporal distribution of the sexes.

Around the world, the reproduction period of *B. capriscus* differs from one region to another, occuring mainly during the warmer months (July–mid-September) in the Gulf of Gabès, during November–December on the coast of Ghana (Ofori-Danson, 1990) and during June–July in the Gulf of Mexico (Wilson *et al.*, 1995) (Figure 6). The water temperature probably plays a major role in oocytes emission.

In general, this period coincides with favourable environmental conditions for the survival and growth of larvae. In fact, low temperature may substantially decrease the chance of survival for fish larvae (Rombough, 1997; Green & Fisher, 2004). In the Gulf of Gabès, the reproduction period of *B. capriscus* begins in May, corresponding to the time when the water temperature increases and the zooplankton productivity is the highest in the Mediterranean (Estrada *et al.*, 1985; Macpherson & Raventos, 2006) and particularly in the Gulf of Gabès (Drira, 2009). Mediterranean subtidal plant communities (algae and seagrasses) begin to develop at this time (Ballesteros, 1991; Alcoverro *et al.*, 1997). This temporal coincidence allows the establishment of young triggerfish which find food resources in addition to the maintenance of rapid growth, development and protection within the subtidal seagrass and algae.

Like many fish species, the gonad index of *B. capriscus* is lower in males than females (Baylis, 1981). In fact, these index values for *B. capriscus* females in Tunisian coasts are higher than those found in the Gulf of Guinea (Stéquert & Gerlotto, 1979). These differences may be related to genetic potential variations and also to food resources availability. This suggests important fertility among individuals in the Gulf of Gabès.

Fish may store the energy required for spawning, in the liver or the muscles. However, the fluctuations of the HSI are relatively synchronous with those of the GSI for both females and males, but no clear relationship between *K* and spawning were found. This suggests that the required energy for spawning might be derived from *B. capriscus* liver accumulating lipid reserves to be spent during laying. However, the muscles do not intervene in supplying the energy for both sexes reproduction.

The size of the first maturity of *B. capriscus* varies from 13 to 30 cm according to location (Table 4). These differences are explained by the fact that the size of mature individuals depends on the biological factors and/or the ecological environment (Wague & M'Bodj, 2002). Human activities such as overfishing (increased fishing effort) can also explain the differences in size (Jennings *et al.*, 2001). Fish subjected to these pressures may have ecophysiological adaptations related to growth or reproduction, dwarfism or early sexual maturity, in order to ensure their survival (Stearns & Crandall, 1984; Olsen *et al.*, 2004).

In *B. capriscus,* females reach their first sexual maturity before males. Similar results have been observed in other species such as triggerfish *Balistes vetula* in Brazil (LF = 23.5 cm female, male 26.5 cm) (Aiken, 1983). This could be explained by the fact that the size of the first sexual maturity is not only linked to environmental factors but also to genetic ones (Wootton, 1998; Sampson & Al-Jufaily, 1999).

The unimodal distribution of GSI suggests that eggs are laid in a single transmission (Garnaud, 1960; Ofori-Danson, 1990; Mackichan & Szedlmayer, 2007). The comparison of *B. capriscus* eggs size, from the Gulf of Gabès, with those

Table 4. Size (cm) at first sexual maturity of *Balistes capriscus* in different regions of the world.

Regions	**Size (cm) at first sexual maturity**	**Reference**
Senegal and Guinea	LF = 13 sexes combined	Gerlotto *et al.* (1979)
Ghana	LF = 14–15 sexes combined	Ofori-Danson (1981)
USA	LF = 30 sexes combined	Manooch (1984)
Ghana	LF = 17–21 sexes combined	Ofori-Danson (1989)
Ghana	LF = 13.5–15.7 sexes combined	Ofori-Danson (1990)
Brazil–São Paulo	LF = 16.9 females LF = 20.0 males	Castro *et al.* (2005)
Brazil	LF = 17 females LF = 20.0 males	Magro *et al.* (2000)
Gulf of Gabès	LF = 20.26 females LF = 21.30 males LF = 20.92 sexes combined	Present study

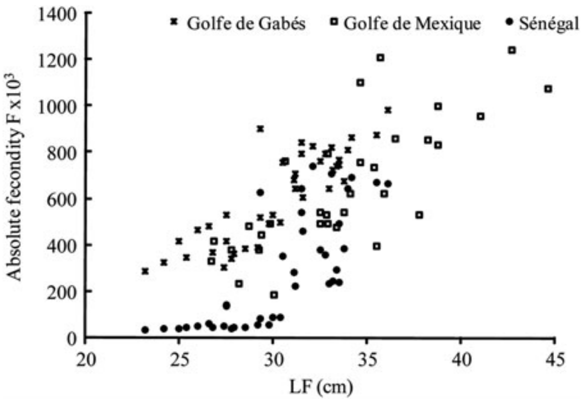

Fig. 7. Comparison of the absolute fecundity of *Balistes capriscus* of the Gabès region with other regions of the world.

from the north-east Gulf of Mexico (Mackichan & Szedlmayer, 2007) does not show any significant difference.

The comparison of the absolute fecundity of *B. capriscus* in the Gulf of Gabès (present study), Senegal (Caverivière *et al.*, 1981) and the Gulf of Mexico (Ingram, 2001) shows significant differences between the three locations (ANOVA, $df_{(3,112)}$ $F = 27.6$, $P < 0.01$) (Figure 7). Absolute fecundity was very similar between the Gulf of Gabès and the Gulf of Mexico. This could be likely explained by the similar climatic conditions in both ecosystems. Absolute fecundity is different and low in Senegal, which is probably related to the small size of *B. capriscus* at the first sexual maturity.

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