

**FECUNDITY AND CONDITION OF SUCCESSFUL INVADERS: *SIGANUS RIVULATUS*
AND *S. LURIDUS* (ACTINOPTERYGII: PERCIFORMES: SIGANIDAE) IN THE EASTERN
MEDITERRANEAN SEA**

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Background. Rabbitfishes, *Siganus rivulatus* and *S. luridus*, are among the most successful invaders in the Mediterranean Sea but population parameters in their new environment are barely known. Fecundity and condition are key parameters of fish populations and their assessment is very important for exotic species; this information is needed to properly evaluate their reproductive and invasive potential. The current study contributes to fill this gap by exploring fecundity and condition of those two fish species.

Materials and Methods. About 1000 individuals of *Siganus rivulatus* and *S. luridus* were processed from off the Lebanese coasts over a 20-month period. Fecundity and condition were estimated and compared. Regression analyses tested the dependence of fecundity on fish length, mass, and gonad mass.

Results. Fecundity values were assessed for *S. rivulatus* and for *S. luridus*: $F_{abs} = 272\,043 \pm 144\,666$ (SD), $F_{rel} = 2123 \pm 808$ oocytes $\cdot g^{-1}$ for *S. rivulatus* and $F_{abs} = 245\,273 \pm 164\,211$, $F_{rel} = 1584 \pm 627$ oocytes $\cdot g^{-1}$ for *S. luridus*. The relation between F_{abs} and gonad mass [g] was $y = 14\,339x + 59\,297$ for *S. rivulatus* and $y = 9245x + 62\,140$ for *S. luridus*. Condition exhibited a clear seasonal trend for the two rabbitfishes. It increased in spring prior to the reproduction period and again in autumn before the decrease of seawater temperature, and remained low during the cold period. Its values were significantly higher for *S. luridus* than to *S. rivulatus*.

Conclusion. *S. rivulatus* displayed a higher fecundity while *S. luridus* showed a better condition in the Eastern Mediterranean. Gonad mass was the best predictor of fecundity for both species while condition exhibited a clear seasonal trend in both rabbitfishes.

Keywords: rabbitfish, *Siganus rivulatus*, *Siganus luridus*, marbled spinefoot, dusky spinefoot, fecundity, condition, Mediterranean, Lebanon

INTRODUCTION

Fecundity and condition are key parameters of fish populations and their assessment is extremely important for exotic species; this information is needed to properly evaluate their reproductive and invasive potential. Rabbitfishes are considered among the most successful invaders in the Mediterranean Sea (Golani et al. 2002, 2004, Galil 2007) and among the worst 100 invasive species in Europe (Anonymous 2008a). At present, two species of rabbitfishes are present in this basin: the marbled spinefoot, *Siganus rivulatus* Forsskål, 1775; and the dusky spinefoot, *Siganus luridus* (Rüppell, 1829). Both are Indo-pacific fishes which entered into the Mediterranean from the Red Sea through the Suez Canal

(Lessepsian migration, Por 1978) and were firstly recorded in 1924 (Steinitz 1927) and 1955 (Ben-Tuvia 1964), respectively. Rabbitfishes have since established large populations in the eastern Mediterranean and have acquired considerable economic importance (Aleem 1969, George 1972, Ben-Tuvia 1985, Papaconstantinou 1990). They have triggered dramatic changes in community structure and in native food webs (Galil 2007) and are competing with native herbivorous fishes such as salema, *Sarpa salpa* (Sparidae), along the Levant coast (Bariche et al. 2004).

The success of rabbitfishes is also confirmed by their geographical spread. Recently *S. rivulatus* was reported from the Adriatic (Dulčić and Pallaoro 2004) and

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S. luridus has settled new populations in the Sicily Channel (Azzurro and Andaloro 2004), extending northwards as far as the Tyrrhenian Sea and the French coast, near Marseilles (Castriota and Andaloro 2005, Anonymous 2008b). Due to their increasing importance in the Mediterranean Sea, various biological and ecological traits of these species have recently been studied or reviewed (Bilecenoglu and Kaya 2002, Bariche et al. 2004, Bariche 2005, 2006, Azzurro et al. 2006, 2007b) and new information now exists on their reproduction (Lahnsteiner and Patzner 1999, Bariche et al. 2003, Azzurro et al. 2007a). However, little and very scattered data has been published regarding their fecundity and condition in the Mediterranean and the Red Sea (Hashem 1983, Amin 1985, Hussein 1986, Azzurro et al. 2007c).

The main aim of this contribution was to collect baseline data on the reproductive potential of *S. rivulatus* and *S. luridus* in the Mediterranean Sea and to integrate it with existing information. The specific objectives were: 1) to estimate fecundity and condition factors of these two rabbitfishes; 2) to reconstruct the relations of these parameters with regard to body size, body weight and gonad weight; 3) to track seasonal variation of condition factors; and 4) to highlight eventual differences between the Mediterranean and the Red Sea populations.

MATERIALS AND METHODS

The study was conducted in the Batrun area (lat 34°15.443' N, long 35°39.435' E), along the northern coast of Lebanon. A total of 528 *S. rivulatus* and 485 *S. luridus* were collected between January 1999 and August 2000. Sampling occurred weekly during the reproductive period and monthly during the rest of the year. Fishes were selected randomly from local fishermen who used trammel nets between 8 and 15 m depth. They were placed on ice and transported immediately to the laboratory for analysis. Total length (L) was measured to the nearest mm and total body mass (M) to the nearest 0.01 g. Gonads were weighed (M_G) to the nearest 0.001 g after fixation in 10% buffered formaldehyde. Ripe gonads (stage III) ovaries were selected according to their macroscopic appearances, following criteria developed in Bariche et al. (2003). Ovaries from 25 ripe female *S. rivulatus* and from 32 female *S. luridus*, captured between 24 May and 21 June 2000, were chosen and dissected. Fecundity was estimated according to the gravimetric method (Holden and Raitt 1974, Murua et al. 2003). The absolute fecundity (F_{abs}) was calculated as the average of the total number of yolked oocytes (following Azzurro et al. 2007a) in three subsamples (0.5–1.0 g) of the same ovary. These three subsamples were selected respectively from the centre and the posterior sides of the right and left gonads and all counts were made under a dissecting microscope. The relative fecundity (F_{rel}) was calculated as $F_{rel} = F_{abs} \cdot M^{-1}$. One-way ANOVA was used to compare relative fecundity among *S. rivulatus* and *S. luridus*. A somatic condition factor (K) was calculated as $K = 100 (M - M_G) \cdot L^{-3}$ for the 20 months study period in order to

detect seasonal variation in physical condition. Regression analyses were conducted to test the dependence of fecundities (F_{abs} and F_{rel}) on different measurements (L , M , and M_G). Comparisons between the two species (Student's t -test) were made on slopes and elevations of the regression lines representing these relationships (Zar 1999). In addition, the ratios $F_{abs}:L$ and $F_{abs}:M$ and M_G were calculated for each of the two species. Means of these ratios were also compared using t -tests for independent samples. Condition indices were also compared using t -tests for independent samples. All statistical tests, including curve-fitting, were performed using SPSS for windows (11.0.0), (copyright©SPSS Inc.) or Microsoft®Excel 2002.

RESULTS

Both absolute (F_{abs}) and relative fecundity (F_{rel}) results were significantly higher in *S. rivulatus* than in *S. luridus*. In *S. rivulatus*, with averages of $F_{abs} = 272\ 043$ oocytes/ovary (SD = 144 666, range = 49 830–708 537) and $F_{rel} = 2123$ oocytes \cdot g $^{-1}$ (SD = 808). In *S. luridus*, averages were $F_{abs} = 245\ 273$ (SD = 164 211, range = 87 476–863 487) and $F_{rel} = 1584$ oocytes \cdot g $^{-1}$ (SD = 627). ANOVA test displayed significantly higher value for *S. rivulatus* than for *S. luridus* ($F_{1,55} = 8.0$; $P < 0.05$).

The relation between fecundity and size is reported in Fig. 1, together with literature data. For *S. rivulatus* individuals larger than 19 and 20 cm L , higher fecundities seem to characterize Mediterranean populations compared to those of the Red Sea.

The relation between the F_{abs} and M and L for both *S. rivulatus* and *S. luridus* species was best described by a power equation ($y = ax^b$) while a linear equation described the relationship between F_{abs} and M_G ($y = a + bx$) (Table 1). M_G was the best predictor of fecundity for both species (Fig. 2). No significant correlations were found between F_{rel} and L , M and M_G measurements for both species.

Comparison between the linear regressions for the two species relating logarithm of F_{abs} to the logarithm L showed that there was no significant difference between the two slopes ($t = 1.260$; d.f. (degree of freedom) = 165; $P = 0.209$), except for *S. rivulatus* having a higher elevation than *S. luridus* ($t = 649.565$; d.f. = 165; $P < 0.01$). A similar comparison logarithm F_{abs} to logarithm M showed a highly significant difference between the two slopes ($t = 13.427$; d.f. = 165; $P \ll 0.01$). Due to this difference in slopes, elevations were not compared. However, the mean (\pm SE, standard error) of the ratio logarithm F_{abs} : logarithm M for *S. rivulatus* (2.59 ± 0.02 , $n = 75$) was shown to be significantly higher ($t = 6.16$, $P < 0.01$) than that of *S. luridus* (2.48 ± 0.02 , $n = 96$). This indicated that, for the same M or L , *S. rivulatus* had a higher F_{abs} than *S. luridus*. Finally, comparison relating F_{abs} to M_G showed again a significant difference between slopes ($t = 2.78$, d.f. = 165, $P < 0.01$). Consequently the comparison of elevations was replaced by the comparison of mean ratios of $F_{abs}:M_G$. A t -test ($t = 3.53$, $P < 0.01$) showed that this ratio was higher for *S. rivulatus*

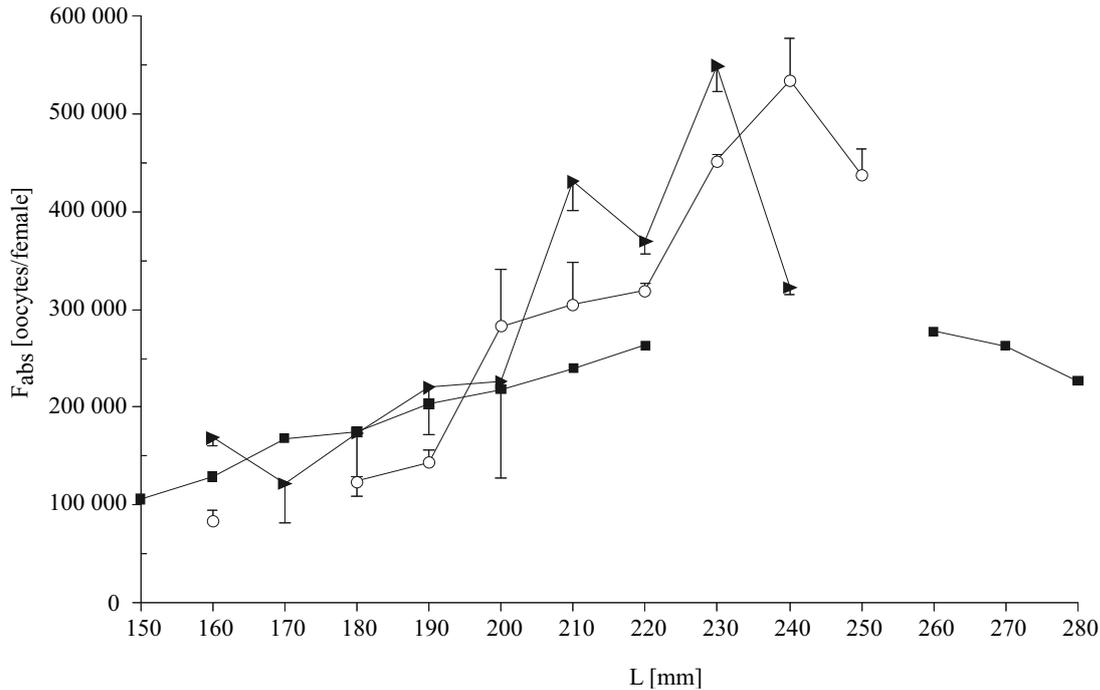


Fig. 1. Variation with sizes of the absolute fecundity for *Siganus rivulatus* (○) and *S. luridus* (▴) and available data for *S. rivulatus* in the Red Sea (■) (Hashem 1983); only one side of the standard deviation (SD) error bar is represented

Table 1

Relations between absolute fecundity (F_{abs}) and total length (L), total mass (M), and gonad mass (M_G) in *Siganus rivulatus* ($n = 75$) and *S. luridus* ($n = 96$)

Species	Relation	r^2	F	P
<i>S. rivulatus</i>	$F_{\text{abs}} = 3.39 L^{3.70}$	0.46	62.74	<0.01
	$F_{\text{abs}} = 552.10 M^{1.26}$	0.45	65.07	<0.01
	$F_{\text{abs}} = 59\,297 + 14\,339 M_G$	0.83	134.60	<0.01
<i>S. luridus</i>	$F_{\text{abs}} = 1.95 L^{3.91}$	0.50	94.58	<0.01
	$F_{\text{abs}} = 215.10 M^{1.38}$	0.59	135.22	<0.01
	$F_{\text{abs}} = 62\,140 + 9245 M_G$	0.75	274.37	<0.01

($19\,605.25 \pm 694.21$, $n = 75$) than for *S. luridus* ($15\,698.21 \pm 861.55$, $n = 96$). The F_{abs} was also higher in *S. rivulatus* than in *S. luridus* for the same M_G .

Sexes were not determined outside the reproduction period since the undeveloped gonads were not identifiable macroscopically. No significant difference in K values was found between male, female and non-mature individuals for both species ($P > 0.05$), except for *S. rivulatus* collected in June 1999 ($t = 2.49$; d.f. = 45, $P = 0.0164$) (Table 2). A mean K value was calculated for all individuals per month (Fig. 3). Maximum K values exhibited similar temporal patterns for *S. rivulatus* and *S. luridus* (Fig. 3). Condition peaked in May 1999 (1.32 ± 0.25 , $n = 26$) and April 2000 (1.50 ± 0.14 , $n = 18$) for *S. rivulatus* and in April 1999 (1.80 ± 0.12 , $n = 18$) and May 2000 (1.74 ± 0.20 , $n = 69$) for *S. luridus*. The K values increased also in the autumn peaking in December 1999 for *S. rivulatus* (1.44 ± 0.09 , $n = 22$) and October 1999 for

S. luridus (1.85 ± 0.15 , $n = 13$) as shown in Fig. 3. Annual mean K was lower for *S. rivulatus*, 1.24 (SD = 0.09), than for *S. luridus* (1.68 ± 0.06). Comparisons made for each of the 20 months (month by month) also showed significant differences ($P < 0.01$) between species.

DISCUSSION

This paper presents a detailed evaluation of the reproductive potential of *S. luridus* and *S. rivulatus* in the Mediterranean Sea. Both rabbitfishes potentially release about 250 000 eggs per spawning season, which represents about 2000 eggs \cdot g $^{-1}$ for *S. rivulatus* and 1500 egg \cdot g $^{-1}$ for *S. luridus*.

Absolute fecundity increased with L and M for both *S. rivulatus* and *S. luridus* according to the equation $y = ax^b$. Values of the constants (a and b) may vary according to the studied population and to environmental variations (Kartas and Quignard 1984). While a describes the popu-

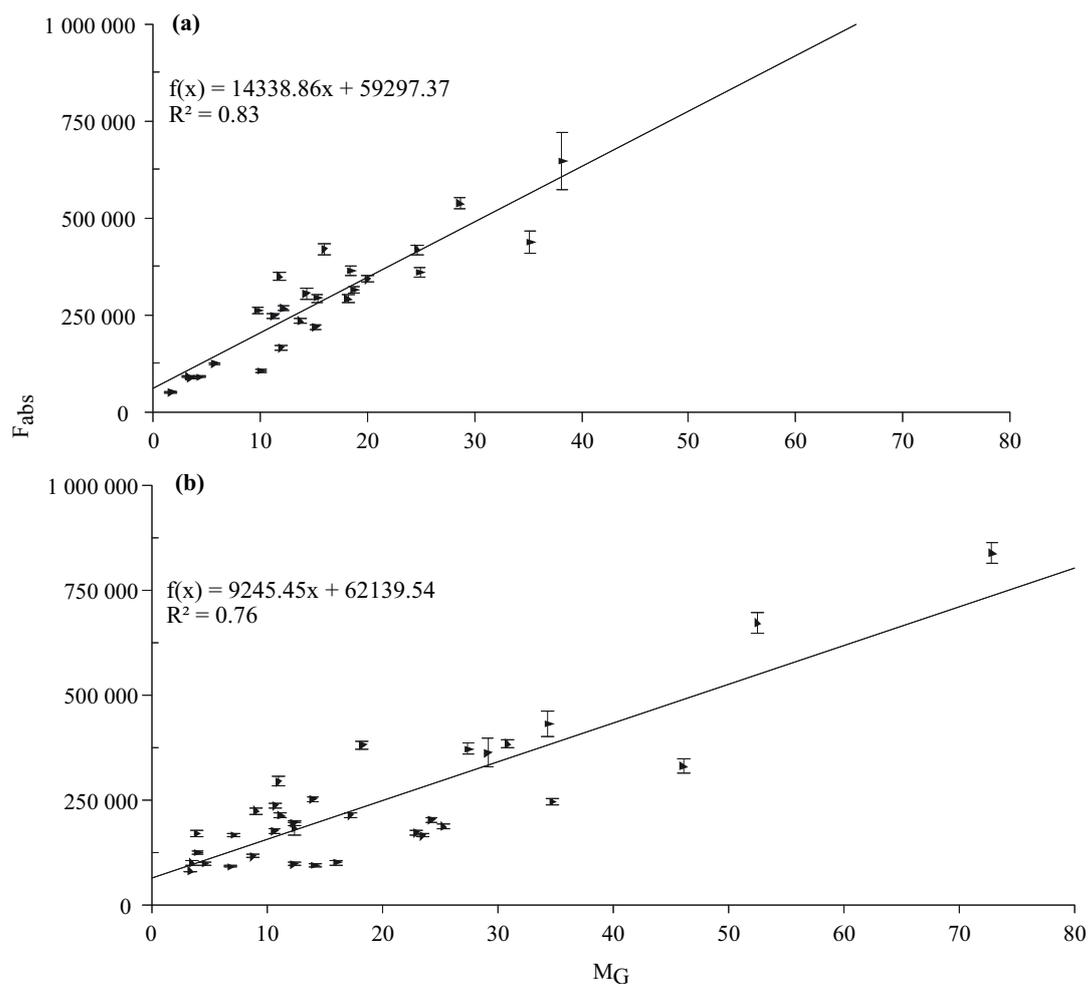


Fig. 2. Absolute fecundity versus gonad mass (M_G) [g] for 25 *Siganus rivulatus* (a) and 32 *S. luridus* (b) sampled from off Lebanon; error bars are standard deviations

Table 2

Monthly values of the condition factor index (mean \pm SD) of *Siganus rivulatus* and *S. luridus* from the Batrun area during the study period; Number of fish analysed in brackets, NA: gender not analysed

Year	Month	<i>Siganus rivulatus</i>			<i>Siganus luridus</i>		
		male	female	NA	male	female	NA
1999	Jan			1.18 \pm 0.10 (15)		1.79 \pm 0.13 (02)	1.63 \pm 0.12 (15)
	Feb		1.27 \pm 0.01 (02)	1.21 \pm 0.13 (26)		1.64 \pm 0.00 (04)	1.63 \pm 0.10 (18)
	Mar		1.06 \pm 0.19 (02)	1.30 \pm 0.12 (13)		1.69 \pm 0.18 (12)	
	Apr	1.17 \pm 0.00 (01)	1.14 \pm 0.06 (07)	1.30 \pm 0.07 (07)	1.84 \pm 0.09 (04)	1.80 \pm 0.14 (10)	1.79 \pm 0.07 (04)
	May	1.34 \pm 0.22 (11)	1.35 \pm 0.16 (09)	1.24 \pm 0.41 (06)	1.59 \pm 0.10 (10)	1.62 \pm 0.15 (08)	
	Jun	1.14 \pm 0.09 (21)	1.24 \pm 0.17 (26)	1.31 \pm 0.09 (02)	1.50 \pm 0.13 (10)	1.53 \pm 0.08 (06)	
	Jul			1.15 \pm 0.22 (20)	1.58 \pm 0.05 (11)	1.55 \pm 0.09 (11)	1.57 \pm 0.00 (01)
	Aug			1.17 \pm 0.19 (25)	1.76 \pm 0.08 (02)	1.81 \pm 0.11 (06)	1.74 \pm 0.07 (05)
	Sep			1.15 \pm 0.12 (22)	1.84 \pm 0.09 (02)		
	Oct			1.21 \pm 0.10 (34)	1.88 \pm 0.14 (08)	1.98 \pm 0.09 (02)	1.69 \pm 0.06 (03)
	Nov			1.19 \pm 0.06 (14)	1.96 \pm 0.12 (03)	1.88 \pm 0.14 (02)	1.57 \pm 0.10 (11)
	Dec			1.44 \pm 0.09 (22)			
2000	Jan			1.07 \pm 0.08 (18)			1.61 \pm 0.26 (10)
	Feb			0.98 \pm 0.12 (18)			1.53 \pm 0.11 (12)
	Mar			1.24 \pm 0.05 (12)	1.63 \pm 0.17 (04)	1.73 \pm 0.11 (10)	1.75 \pm 0.10 (04)
	Apr			1.50 \pm 0.14 (18)	1.71 \pm 0.14 (18)	1.77 \pm 0.15 (23)	1.67 \pm 0.04 (06)
	May	1.34 \pm 0.20 (23)	1.42 \pm 0.13 (17)	1.60 \pm 0.33 (02)	1.74 \pm 0.22 (19)	1.74 \pm 0.21 (37)	1.74 \pm 0.10 (12)
	Jun	1.20 \pm 0.18 (42)	1.25 \pm 0.17 (28)		0.61 \pm 0.15 (40)	1.70 \pm 0.20 (66)	1.74 \pm 0.00 (01)
	Jul			1.16 \pm 0.19 (30)	1.57 \pm 0.05 (19)	1.55 \pm 0.09 (14)	1.57 \pm 0.00 (01)
	Aug			1.20 \pm 0.21 (35)	1.77 \pm 0.06 (03)	1.80 \pm 0.10 (10)	1.77 \pm 0.08 (06)
	<i>n</i>	98	91	339	153	223	109

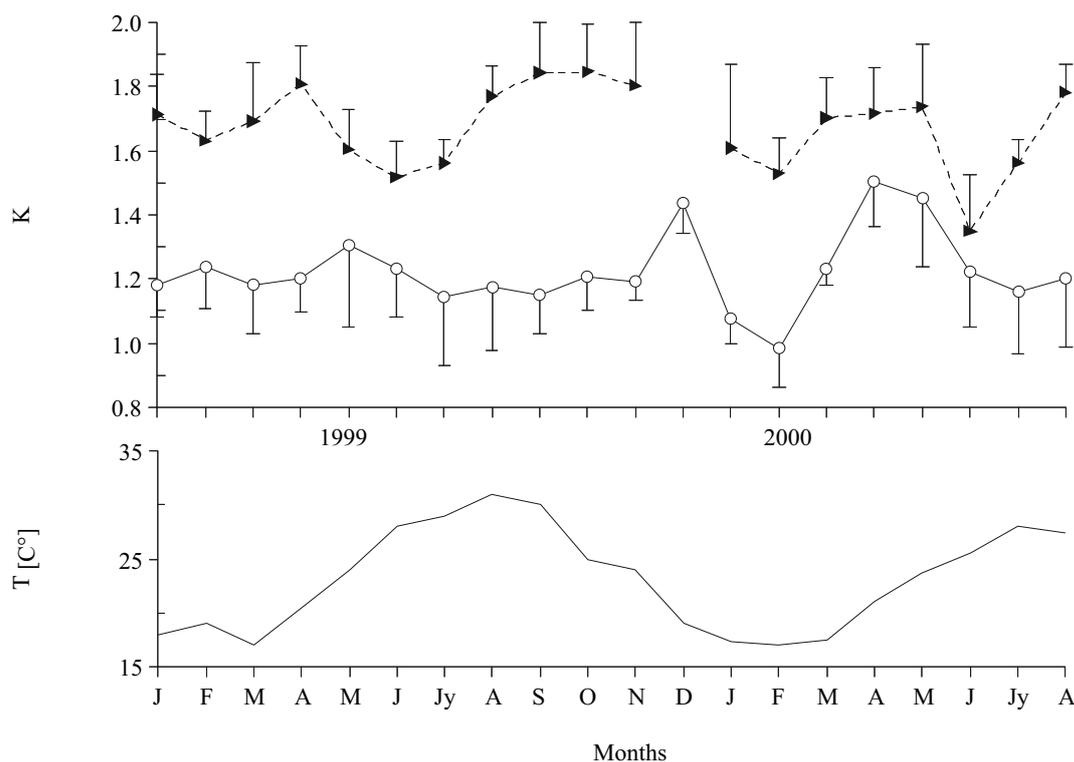


Fig. 3. Monthly variation in (a) the mean condition factor index of *Siganus rivulatus* (\circ) and *S. luridus* (\blacktriangleright) in the Batrun area from January 1999 to August 2000 and (b) surface water temperature in Lebanon during the same period (Bariche et al. 2003). Only one side of the standard deviation (SD) error bar is represented

lation fecundity, b shows the nature of the allometry between L and F_{abs} . The b values of 62 fish species compared by Wootton (1979) showed that b fluctuated between 1 and 7 with a modal value at about 3.25–3.75. Values found in this study are in accordance with the mode range and showed that F_{abs} grew proportionally to 3.70 times and 3.91 times the lengths of *S. rivulatus* and *S. luridus* respectively. Similarly, F_{abs} increased with the M ($b = 1.26$ for *S. rivulatus*; $b = 1.38$ for *S. luridus*). An exponent value close to one, such as in the present study, indicates that fecundity grows proportionally to body mass (Kartas and Quignard 1984). According to these authors, fish condition, which varies with region or year, has an important influence on the relation of F_{abs} to M . For both species, F_{abs} was best described by a linear relationship to M_G which thus provided the most straightforward indicator of fecundity. These regressions are generally influenced by age and environmental conditions (Kartas and Quignard 1984). This is in accordance with the results of the present study where largest (i.e., oldest) individuals presented higher fecundities (Fig. 1).

Regarding *S. luridus*, information presented in this study is original and no comparison is possible between invasive and native populations. Recently, *S. luridus* was shown to spawn from May to July in the eastern Mediterranean and has been defined as a ‘group synchronous spawner’ (Bariche et al. 2003, Azzurro et al. 2007a), but in both Mediterranean and Red Sea populations it

remains important to assess whether one or multiple batches of oocytes reach maturity (Azzurro et al. 2007c). Should the second case prove correct, calculated absolute fecundities in this study for *S. luridus* should be then considered as ‘batch fecundities’.

As opposed to its congeneric *S. luridus*, some information exists on the fecundity of Red Sea *S. rivulatus*, but, most likely due to different samplings and/or methodologies, as well as lack of some size classes, it is difficult to make appropriate comparisons and no one coherent pattern can be concluded. Oddly, at small sizes (≤ 190 mm L) invasive *S. rivulatus* showed lower fecundities with respect to native populations, while for larger size classes the opposite was true (Fig. 1). In addition, fecundities from Red Sea specimens ranging from 230 to 250 mm L are absent (Hashem 1983). Conclusions are thus contradictory and without any apparent logical explanation, and specific studies are requested to compare the fecundity of Mediterranean and Red Sea rabbitfishes. This would be important to test for eventual reproductive changes in the new environment.

Our study assessed the fecundity values in the two species, *S. rivulatus* and *S. luridus*, that displayed a different invasive potential in the eastern Mediterranean Sea, the former species being the most abundant and successful (George 1972, Bariche et al. 2004). Generally speaking, it is extremely difficult to identify those biotic and abiotic variables that lead to becoming a successful invad-

er. However we know that some of these variables are key determinants for the dispersal success of Lessepsian fish species (Ben Rais Lasram et al. 2008) and that fecundity has been indicated among the most discriminating life-history traits to explain the success of invasive fish species (Vila-Gispert et al. 2005). In this case, the higher fecundity of *S. rivulatus* compared with that of *S. luridus* would confirm the importance of this parameter in the new environment.

Information on the condition of these rabbitfishes helped to interpret and discuss our fecundity data. The condition factor is directly related to environmental conditions (Clesceri et al. 1999) and changes in *K*, for several fishes have been ascribed to a depletion of body reserves during gonad maturation (Htun-Han 1978). In the current study, condition peaked in May 1999 and then again in April–May 2000, which represented the period of pre-gonadal development for both species. The *K* values decreased in June and July when the species were spawning (Bariche et al. 2003). This situation was similar for both species in Red Sea populations (Hashem 1983) where maximum *K* is reached before gonad maturation and then drops after spawning. In both rabbitfish populations studied, *K* values also reached a maximum in the autumn, which corresponded with the start of the cold period. Then it decreased gradually and reached a minimum in February, the month where the Lebanese seawater temperature was lowest (Fig. 3). Finally, *K* variations in this study were more important in 2000 than in 1999 for both species. This might indicate that factors other than temperature might have fluctuated more in 2000 than in 1999. There are no indications whether or not *K* changed in the Mediterranean, as data from the Red Sea is scarce and incomplete. Finally, *S. rivulatus* appeared to have a lower overall *K* value than *S. luridus*. The difference in elevation between the two lines is certainly attributable to the morphology of the species, with *S. luridus* having a greater body depth.

Intraspecific variation in fecundity and condition exists in populations living in different environments (Nikolsky 1969, Moyle and Cech 2004). The Levantine basin has provided suitable environmental conditions for Lessepsian rabbitfishes in terms of physical factors (e.g., temperature and salinity ranges) and habitat but also in low competition pressure and high food availability resulting from the low diversity and abundance of competing herbivores in the Mediterranean. In addition, predation on rabbitfishes in the Mediterranean seems to be very moderate. All of these factors have enhanced various life history parameters such as reproduction, growth and settlement making them very successful in the eastern Mediterranean.

Finally, the current geographical expansion of both exotic and native thermophilic fish species in the Mediterranean is considered as clear signals of climate warming (Francour et al. 1994, Ben Rais Lasram et al. 2008, Azzurro 2008 and references therein included).

According to the predicted increase of temperature (1–3°C) in the Mediterranean by the end of the 21st cen-

ture (Somot et al. 2006) it is expected that species such as rabbitfishes will further enhance their expansion northwards affecting more and more the Mediterranean Sea ecosystem.

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