

Annual reproductive cycle and fecundity of *Scorpaena notata* (Teleostei: Scorpaenidae)*

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SUMMARY: *Scorpaena notata* (Teleostei: Scorpaenidae) is an oviparous species with external fertilisation that shows some unusual features in its gonadal morphology and gametogenesis. In this work we analyse the annual reproductive cycle and the fecundity of this species by studying the monthly histological changes in the gonads and of various indices related to reproduction. Sexual dimorphism does not occur in the population we studied, which is clearly dominated by males. Multiple spawning takes place between July and October, consisting of between 6,000 and 33,000 eggs per female, each of about 500 μm in diameter. The fecundity of the species is determined by the size and weight of the individuals.

Keywords: scorpionfish, reproduction, annual cycle, fecundity.

RESUMEN: CICLO REPRODUCTIVO ANUAL Y FECUNDIDAD DE *SCORPAENA NOTATA* (TELEOSTEI: SCORPAENIDAE). – *Scorpaena notata* (Teleostei: Scorpaenidae) es una especie ovípara de fertilización externa que presenta algunas características peculiares en su morfología gonadal y gametogénesis. En este trabajo se analiza el ciclo reproductivo anual y la fecundidad de dicha especie, mediante el estudio de los cambios histológicos mensuales que muestran las gónadas a lo largo del ciclo anual así como de diversos índices relacionados con la reproducción. La población analizada no presenta dimorfismo sexual, aunque el número de machos es muy superior al de hembras. La puesta múltiple ocurre entre los meses de Julio y Octubre y consiste de entre 6000 y 33000 huevos por hembra, de unos 500 μm de diámetro. La fecundidad de la especie viene determinada por el tamaño y el peso de los ejemplares.

Palabras clave: escórpora, reproducción, ciclo anual, fecundidad.

INTRODUCTION

The family Scorpaenidae is of particular interest from the reproductive point of view, since it is made up of species with a wide variety of reproductive strategies, ranging from the most basic oviparity to matrotrophic viviparity. Wourms and Lombardi (1992) consider that, specifically within the genus *Scorpaena*, there is a shift from a primitive to a specialized mode of oviparity. Fertilization is still external and development is ovuliparous, but eggs are embedded in a gelatinous matrix.

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Scorpaena notata Rafinesque 1810 is a common species in rocky coastal habitats, and is found at depths of up to 700 meters. It is the object of semi-industrial and small-scale fishing (Whitehead *et al.*, 1986; Fischer *et al.*, 1987). It appears in the Mediterranean Sea and adjacent areas of the Atlantic, Madeira, the Azores and the Cabo Verde Islands. The southern limit of distribution seems to be Senegal (Eschmeyer, 1969). Until recently, most aspects related to its reproduction were unknown, but a recent study into its ovarian structure and process of oogenesis (Muñoz *et al.*, 2002a) revealed that it is an ovuliparous species that shows several features that can be considered intermediate

between the most basic oviparity and the first transitional stages towards viviparity.

Muñoz *et al.*, (2002b) have already examined the histology of this species and the ultrastructure of the testes and the spermatogenic phases. These authors showed that the gonadal structure is intermediate between the restricted and unrestricted spermatogonial types of testes defined by Grier (1981, 1993) and that the spermatogenesis is semicyclic, which has been described in very few species of fish.

In this study, we aim to provide an in-depth analysis of the annual cycle of *S. notata* by studying the seasonal histological changes of the gonads and of various indices related to its reproduction. We also estimate and explain the fecundity of this species in relation to its specialized reproductive strategy.

MATERIALS AND METHODS

For the description of the different stages of maturity of the gonads, the ovaries and the testes were embedded in Histosec 56-58 pF (Merck) or in hydroxyethyl methacrylate, and were sectioned at between 4-10 μm , depending on the sex and the stage of maturity. Transverse and longitudinal sections were obtained for both sexes. The following stains were used for the samples kept in Histosec: haematoxylin-eosin for general histology; Mallory as a trichrome; PAS reaction (periodic acid-Schiff) for the demonstration of neutral mucopolysaccharides; and Alcian blue for acid mucopolysaccharides. The samples kept in methacrylate were stained with methylene blue-basic fuchsin, toluidine blue, and also PAS.

The stages of development in the oocytes were determined by following the criteria established by Wallace and Selman (1981) and West (1990). The ovaries were classified according to the more developed type of oocyte (West, 1990). The development stage of the testis was determined following the criteria laid down by Grier (1981).

In order to study the indices related to reproduction, we used 507 individuals of *Scorpaena notata* which were caught during a year-long period at various ports along the Costa Brava (northwest Mediterranean). The fish were fixed immediately after capture in 10% formaldehyde and preserved in 4% formaldehyde. The following parameters were analysed:

- Sexual dimorphism. The total standard lengths and weights of the males and females were compared using an analysis of variance (ANOVA).

- Sex Ratio (SR = Number of males / Number of females) and the monthly variations of this index. We determined if the result was significantly different from 1 by means of the χ^2 test.

- The gonadosomatic index (GSI = weight of gonad x 100 / eviscerated weight), the hepatosomatic index (HSI = weight of liver x 100 / eviscerated weight) and the condition factor (K = eviscerated weight x 100 / standard length³).

All the indices were calculated as a function of the eviscerated weight, in order to avoid possible variations arising from differences in the digestive tract contents or energy reserves of the specimens. We calculated the indices, separating the fish according to sex and month of capture. Later, we observed any significant differences in the monthly variations by means of an analysis of variance (ANOVA). All the statistical analyses in this section were carried out in line with the criteria set out by Sokal and Rohlf (1995) with the programme SPSS 12.0S for Windows.

Fecundity was estimated in 45 females using the gravimetric method (Burd and Howlett, 1974; Hunter *et al.*, 1985). The oocytes were separated by introducing samples of completely mature ovaries into Gilson's solution, as modified by Simpson (1951). The eggs were then filtered and once they had been sorted into different diameters they were counted. We repeated the process twice for each ovary. The individual or absolute fecundity refers to the number of eggs produced per female per year (Wootton, 1979), and can be defined as the number of mature oocytes present in the ovary immediately before spawning (Bagenal, 1973). In species that use multiple spawning, it is the number of oocytes destined for spawning, i.e. the ones that will mature during the current reproductive cycle, which are usually taken into account (Aboussouan and Lahaye, 1979). Therefore only oocytes with a diameter greater than the oocytes at the cortical alveoli stage were taken into account, since only these are considered to have been released in this reproductive cycle. This absolute fecundity tends to increase according to the size and age of the fish. Therefore, in order to facilitate the comparison we also calculated the relative fecundity, i.e. the number of eggs per unit eviscerated weight (Bagenal, 1978). In order to study the relationship between the fecundity and the size or the total weight of the individual, we used the linear regression analysis by means of the logarithm $\log Y = \log a + b \cdot \log X$. This is calculated using the least squares method and corre-

sponds to an exponential function of the type: $Y = a \cdot X^b$. The significance levels are the same as we described above. Finally, we also determined the frequency distribution of the egg diameters.

RESULTS

Seasonal histological changes in the gonads

Testes

The lobular structure of the testes can be seen clearly during November and December, since they are in the *spermatogonial proliferation period*. According to Grier (1981), they are characterized by the fact that the lobular lumens only contain a few spermatogonial cysts here and there on the periphery, which are always enclosed in the Sertoli cells which cover the inside of the seminiferous lobule. During the months between January and May, the testes are in the *early recrudescence period*: the lobular lumens are full of spermatocytes, and usually free of cysts (Fig. 1A). In May, the testes enter the *mid-recrudescence period*, and now contain germinal cells in all stages of development: spermatogonia, spermatocytes and spermatids. Already little groups of free spermatozoa can be seen in the lobular lumen (Fig. 1B). From June onwards, the lobules still show all the cited stages, but especially spermatids in various stages of development as well as spermatozoa: the testes are in the *late recrudescence period* (Fig. 1C). During the *functional maturity period*, which occurs from July to September, the lobules and all the ducts are full of sperm. A great quantity of PAS negative substance is detected within the lobular lumens (Fig. 1D). Finally, in September, there are no spermatozoa in any ducts or other regions of the testes because they are now in the *post-spawning period*. Spermatogonia become more and more abundant.

Ovaries

From November to March, oogonia and oocytes at various stages of development can be observed. This is the *period of previtellogenesis* (Fig. 1E). The *vitellogenic period* begins approximately in June, when the largest oocytes exhibit yolk granules that grow progressively (Fig. 1F). During the *period of maturation*, between July and October, a lot of mature oocytes which are full of yolk granules as well as oocytes with migrated germinal vesicle and hydrated oocytes are detected (Fig. 1G). The ovary also contains postovulatory follicles, so it can therefore be assumed that spawning takes place within this period. During the periods of vitellogenesis and spawning, the internal epithelium of the ovarian wall has cytoplasmic projections and the lumen of the ovary contains PAS positive ovarian fluid, which is particularly abundant and viscous during spawning (Fig. 1H).

Reproductive indices

Table 1 shows the averages obtained for the standard lengths and total weights of the males and females of *Scorpaena notata*. There are no significant differences between the values obtained for the two sexes.

The annual and monthly sex ratio values are shown in Table 2: 60.7% of the 507 individuals are male and the remaining 39.3% female, so the sex ratio is 1.5 which differs in a highly significant way from 1 ($c^2=24.434$, g.d.l.=1, $p=0.000$).

Figure 2 shows the annual development of the various indices we analysed in relation to the phase the gonad is in. The gonadosomatic index (GSI) shows highly significant differences for both sexes (ANOVA, $p=0.000$), and the maximum values appear between June and October in males, and between July and September in females. For the hepatosomatic index (HSI), which also shows high-

TABLE 1. – Standard length (SL, in mm) and total weight (TW, in g) of *Scorpaena notata*. (n.s. = no significant differences, $p>0.05$)

	n	mean \pm SE	minimum	maximum	SD	significance
SL						
males	308	116.2 \pm 0.8	73.0	147.0	14.87	
females	199	114.2 \pm 1.3	71.0	167.0	18.46	
total	507	115.4 \pm 0.7	71.0	167.0	16.38	n.s.
TW						
males	308	73.6 \pm 1.6	13.9	160.0	28.08	
females	199	72.8 \pm 2.5	15.1	231.5	35.84	
total	507	73.3 \pm 1.4	13.9	231.5	31.33	n.s.

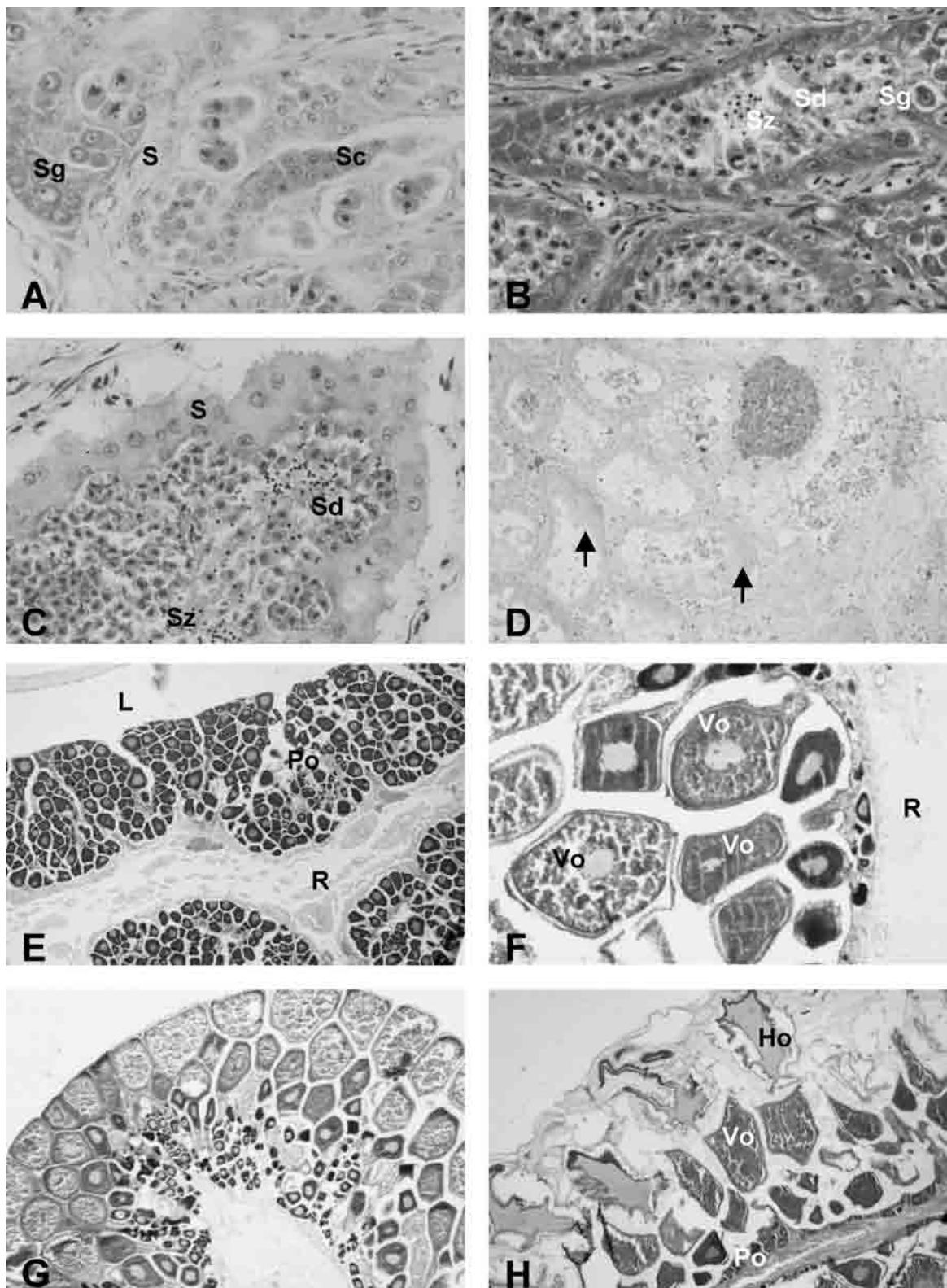


FIG. 1. – Seasonal histological changes in the gonads of *Scorpaena notata*. A-D: Histological sections of the testis. A: Early recrudescence period. B: Mid recrudescence period. C: Late recrudescence period. D: Functional maturity period. Arrows show the testicular fluid within the lobular lumens. (S: Sertoli cell; Sc: spermatocytes; Sd: spermatids; Sg: spermatogonia; Sz: spermatozoa). E-F: Histological sections of the ovary. E: Previtellogenic period. F: Vitellogenic period, with several stages of vitellogenesis. G: Maturation period. H: Late stage of maturation period, with a lot of hydrated oocytes. Note the ovarian fluid between oocytes. (L: ovarian lumen; Ho: hydrated oocyte; Po: previtellogenic oocyte; R: ovarian rachis; Vo: vitellogenic oocyte).

TABLE 2. – Monthly sex ratio values in *Scorpaena notata*. (n.s. = no significant differences, $p>0.05$; * = significant differences, $p<0.05$; ** = highly significant differences, $p<0.001$)

	n	males %	N	females %	χ^2	significance
January	24	75.0	8	25.0	8.000	* (0.005)
February	15	48.4	16	51.6	0.032	n.s. (0.857)
March	17	65.4	9	34.6	2.462	n.s. (0.117)
April	43	72.9	16	27.1	12.356	** (0.000)
May	19	73.1	7	26.9	5.538	* (0.019)
June	16	80.0	4	20.0	7.2000	* (0.007)
July	31	51.7	29	48.3	0.067	n.s. (0.796)
August	28	59.6	19	40.4	1.723	n.s. (0.189)
September	18	43.9	23	56.1	0.610	n.s. (0.435)
October	25	49.0	26	51.0	0.020	n.s. (0.889)
November	28	59.6	19	40.4	1.723	n.s. (0.189)
December	44	65.7	23	34.3	6.582	* (0.010)
annual	308	60.7	199	39.3	23.434	** (0.000)

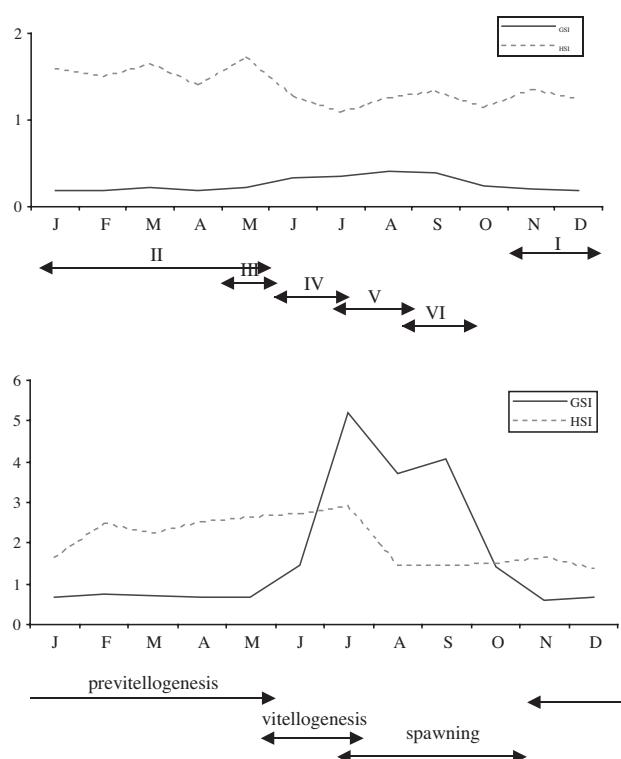


FIG. 2. – Annual cycle of *Scorpaena notata*. The graphs show the annual development of the indices related to reproduction. Below each graph are details of the stage which the gonads are going through. The testes have the following stages: (I) spermatogonial proliferation, (II) early recrudescence, (III) mid recrudescence, (IV) late recrudescence, (V) functional maturity and (VI) post spawn.

ly significant monthly changes (ANOVA, $p=0.000$), the highest values appear from January to May in males, and from January to July in females. The condition of the individuals we studied (K) showed highly significant differences among the males but no significant differences among the females (ANOVA, $p=0.000$ and $p=0.256$, respectively). The profile of the condition factor is not shown in Figure

TABLE 3. – Absolute and relative fecundity of *Scorpaena notata*. (Abs. F = absolute fecundity, M = month; Rel. F = relative fecundity, SL = standard length, in mm; TW = total weight in g).

M	SL	TW	Abs. F	Rel. F
7	123	88.3	15389	203.5
7	119	92.2	23153	302.6
7	122	86.0	21708	287.9
7	110	61.4	15914	306.0
7	121	91.1	11108	140.6
7	122	84.0	22407	313.4
7	142	147.9	32850	266.8
7	140	131.9	32756	297.8
7	123	95.7	6026	69.5
7	142	134.1	22833	192.0
7	128	95.9	20063	242.3
7	114	68.7	12322	204.7
7	110	57.0	8900	178.0
7	119	76.8	11536	178.3
7	140	137.0	23097	204.4
7	117	80.8	16182	227.9
7	140	133.0	15554	135.1
7	131	118.8	15589	154.0
7	104	55.8	15767	324.4
7	134	118.3	18796	184.8
7	132	115.1	20217	202.2
8	119	72.3	19865	314.3
8	129	90.5	11352	138.1
8	113	68.8	9635	157.9
8	117	67.0	13566	226.1
8	115	57.5	9475	185.4
8	107	60.3	12155	237.4
8	115	70.3	14240	235.4
8	106	56.2	9843	201.3
8	94	35.8	6048	192.0
9	119	67.9	13131	218.1
9	127	102.1	9785	104.9
9	141	125.2	12374	110.9
9	123	89.9	5807	73.9
9	149	134.6	11608	95.6
9	102	46.4	7090	170.4
9	126	93.4	13135	160.6
9	128	90.2	15370	193.8
9	151	172.6	19275	127.9
9	129	101.7	18209	221.8
9	116	64.2	12613	222.4
9	115	61.1	9288	171.7
9	152	175.4	12747	80.6
9	118	72.5	15079	240.9
10	113	61.8	19911	396.6

2 because in both sexes the annual development of the index is not very marked, with only slight decreases during late summer. Mesenteric fat was not detected in any of the specimens analysed.

Fecundity

The results obtained for absolute and relative fecundities are presented in Table 3. The distribution of the eggs in terms of frequencies of diameters is relatively open and often marked by two peaks. The relationship of the absolute and relative fecundity with the size and total weight of the specimens was significant in all cases.

DISCUSSION

During November, for *Scorpaena notata* both the ovaries and the testes are in the initial phases of development. In January, the hepatosomatic index (HSI) of the females begins to increase continuously and constantly, reaching much higher values than in the case of the males, but this is a common feature in many species of fish.

The males enter a phase of mid-recrudescence in May, which leads to a progressive increase in testicular activity as well as a significant decrease in their HSI. In the case of the females, the growth in GSI is more sudden and occurs later, beginning in July, which also brings with it a sharp fall in HSI in the following month. The transitory increase in the relative weight of the liver just before the increase in weight of the gonads suggests mobilization and processing of fatty acids and carbohydrates (Bruslé and González, 1996).

The spawning period of the scorpionfish is clearly delimited between July and October, a period which coincides, although it is slightly longer, with the period given for the Gulf of Leon (Duclerc and Aldebert, 1968) and the Algiers region (Siblot-Bouteflika, 1976). On the other hand, Fischer *et al.*, (1987) stated that the reproduction of this species in the Mediterranean probably occurs in May, a hypothesis which we consider to be erroneous.

The condition of the individuals does not seem to be affected much by reproductive activity. The explanation probably lies in the major importance of the liver as an organ for storage, since no mesentery fat reserves were detected, nor were there seasonal changes in alimentary behaviour (Harmelin-Vivien *et al.*, 1989) that could alleviate such a drain on

resources. In the same vein, Shchepkin (1971) found that the liver of *S. porcus* had a high fat content compared to the muscles, and pointed out the major role of the liver as an organ for storing reserves to be used during reproduction. This information and the results about the evolution of the HSI obtained here suggest that the liver of the scorpionfish is the main provider of energy during the maturation and spawning periods.

The population we studied of *Scorpaena notata* is clearly dominated by males. The proportion of males is also higher in the Algiers region (Siblot-Bouteflika, 1976) and in Marseille (Kaim-Malka and Jacob, 1985), although the difference is not as marked as it is in this study. In contrast, Bradai and Bouain (1991) studied the reproduction of two species of the same genus and found that, while *S. scrofa* had similar numbers of males and females, the population of *S. porcus* was clearly dominated by females, especially among larger-sized individuals. These authors felt that the results indicated a faster growth rate in the *S. porcus* females, a characteristic also attributed to *S. guttata* (Love *et al.*, 1987). In the case of *S. notata*, the large inequality in the sex ratio cannot be connected with sexual differences in growth rates, since male dominance appears above all in medium-sized individuals (Muñoz *et al.*, 1996). Furthermore, the morphometric analysis carried out showed no significant variations in size between males and females. However, the sex ratio obtained from a monthly population analysis also rules out the segregation of the sexes during spawning, a behaviour which in some species leads to different sex ratios of the unit (deMartini and Fountain, 1981; Alheit *et al.*, 1984; Barbieri *et al.*, 1992; among others). One possible explanation would be the existence of different distribution patterns between males and females, but there is insufficient data to confirm this idea.

When *Scorpaena notata* spawns, the number of eggs per female ranges from approximately 6000 to 33000. The analysis of the fecundity of another species of the same genus, *S. porcus*, carried out by Bradai and Bouain (1991), gave similar figures for total egg number and distribution of frequencies of diameters. The distribution of oocytes in various stages of development indicates that spawning is multiple, in such a way that the release of the more mature group is followed by the development and spawning of the following group. If we compare similar-sized individuals of *S. notata* captured at the beginning and end of the reproductive period (exam-

ples with standard length = 140 mm from July and examples with standard length = 141 from September), we can see that the total egg number per female decreases as the spawning period goes on, a characteristic feature of a species with a determined fecundity (Greer Walker *et al.*, 1994). At the same time, the decrease in relative fecundity would also make the worsening condition of the individuals clear, as a result of the drain on resources brought about by reproduction. These tendencies remain even if the individuals from September are larger (examples with standard length = 149 or 152), despite the fact that fecundity increases significantly as the standard length and the weight of the fish increases.

It should be noted that the fecundity of *S. notata* is relatively low compared with other species from the same Scorpaeniformes order, whether they are typically oviparous species, such as *Trigla lyra* (Muñoz *et al.*, 2002c), with a maximum number of eggs which our own studies found to be around 108000 per female (Muñoz, 2001), or whether they are species of a much more viviparous nature, such as the zygotrophic species *Helicolenus dactylopterus*, with a maximum egg count of 87000 per female (Muñoz and Casadevall, 2002). This low fecundity may be related to the specialized reproductive behaviour of the species studied in this paper. *S. notata* releases the spawn within a gelatinous mass segregated by an internal epithelium of the ovarian wall, which may have various functions, such as that it enables the spawn to float as well as provides mechanical protection and defence against predators (Muñoz *et al.*, 2002a). However, if we combine the data we obtained with the data from our previous work on testicular structure and spermatogenesis of the same species (Muñoz *et al.*, 2002b), another function of this gelatinous mass, which is perhaps the most important, becomes apparent: it keeps the spawn together. The abundant, viscous seminal fluid probably keeps the sperms together when they are released. If they are released onto the grouped mass of eggs within the gelatinous matrix, fertilization is assured, therefore reducing the need for the female to produce numerous eggs which would explain the low fecundity of the species. Observations on mating scorpionfish during certain times of the year seem to bear out this hypothesis.

It has been observed that the maximum egg diameter of *Scorpaena notata* is about 500 mm. This figure was obtained by both histological measurement and after being fixed in Gilson liquid.

However, it must be pointed out that the eggs of the same species that were found in the sea, floating within the gelatinous matrix, measured between 760 and 880 mm (Spartà, 1956; Kimura *et al.*, 1989). This difference in size is probably partly due to the decrease in volume of the oocytes that occurs when they are fixed in formalin (between 0 and 10% according to Fleming and Ng, 1987; Hislop and Bell, 1987; Lowerre-Barbieri and Barbieri, 1993), as well as the significant increase in volume in the eggs of some species when they come into contact with the marine environment.

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REFERENCES

- Aboussouan, A. and J. Lahaye. – 1979. Les potentialités des populations ichthyologiques. Fécondité et ichtyoplancton. *Cybium*, 6: 29-46.
- Alheit, J., V.H. Alarcon and B.J. Macewicz. – 1984. Spawning frequency and sex ratio in the Peruvian anchovy, *Engraulis ringens*. *Calif. Coop. Fish. Invest. Rep.*, 25: 43-52.
- Bagenal, T.B. – 1973. Fish fecundity and its relations with stock and recruitment. *Rapp. P.-V. Réun. Com. Int. Explor. Scient. Mer Méditerr.*, 164: 186-198.
- Bagenal, T.B. – 1978. Aspects of fish fecundity. In: S.D. Gerking (ed.), *Ecology of freshwater fish production*, pp. 75-101. Blackwell, Oxford.
- Barbieri, L.R., R.P. Dos Santos and J.V. Andreatta. – 1992. Reproductive biology of the marine catfish, *Genidens genidens*, in the Jacarepaguá Lagoon system, Rio de Janeiro, Brazil. *Environ. Biol. Fishes*, 35: 23-35.
- Bradaí, M.N. and A. Bouain. – 1991. Reproduction de *Scorpaena porcus* (Linné, 1758) et de *Scorpaena scrofa* (Linné, 1758) (Pisces, Scorpidae) du Golfe de Gabes. *Oebalia*, 17: 167-180.
- Bruslé, J. and G. González. – 1996. The structure and function of fish liver. In: J.S. Munshi and H.M. Dutta (eds.), *Fish Morphology*, pp. 77-93. Oxford and Ibh, New Delhi.
- Burd, A.C. and G.J. Howlett. – 1974. Fecundity studies on North Sea herring. *J. Cons. Perm. Int. Explor. Mer*, 35: 107-120.
- DeMartini, E.E. and R.K. Fountain. – 1981. Ovarian cycling frequency and batch fecundity in the queenfish, *Seriurus politus*: attributes representative of serial spawning fishes. *Fish. Bull.*, 79: 547-560.
- Duclerc, J. and Y. Aldebert. – 1968. Remarques sur la biologie et l'écologie des Scorpénidés du golfe du Lion. *Rapp. P.-V. Réun. Com. Int. Explor. Scient. Mer Méditerr.*, 19 (2): 251-252.
- Eschmeyer, W.N. – 1969. A systematic review of the scorpionfishes of the Atlantic Ocean (Pisces: Scorpidae). *Occas. P. Calif. Acad. Sci.*, 79: 1-130.
- Fischer, W., M. Schenck and M.L. Bauchot. – 1987. *Fiches FAO d'identification des espèces pour les besoins de la pêche. Méditerranée et mer Noire*. FAO, Rome,
- Fleming, I.A. and S. NG. – 1987. Evaluation of techniques for fixing, preserving, and measuring salmon eggs. *Can. J. Fish. Aquat. Sci.*, 44: 1957-1962.
- Greer Walker, M., P.R. Witthames and I. Bautista de los Santos. – 1994. Is the fecundity of the Atlantic mackerel (*Scomber scombrus*: Scombridae) determinate? *Sarsia*, 79: 13-26.
- Grier, H.J. – 1981. Cellular organization of the testis and spermatogenesis in fishes. *Amer. Zool.*, 21: 345-357.

- Grier, H.J. – 1993. Comparative organization of Sertoli cells including the Sertoli cells barrier. In: L.D. Russel and M.D. Griswold (eds.), *The Sertoli Cells*, pp. 703-739. Clearwater, Cache River Press, FL.
- Harmelin-Vivien, M.L., R.A. Kaim-Malka, M. Ledoyer and S.S. Jacob-Abraham. – 1989. Food partitioning among scorpaenid fishes in Mediterranean seagrass beds. *J. Fish Biol.*, 43: 715-734.
- Hislop, J.R.G. and M.A. Bell. – 1987. Observations on the size, dry weight and energy content of the eggs of some demersal fish species from British marine waters. *J. Fish Biol.*, 31: 1-20.
- Hunter, J.R., N.C.H. Lo and R.J.H. Leong. – 1985. Batch fecundity in multiple spawning fishes. In: R. Lasker (ed.), *An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy, Engraulis mordax*, pp. 67-77. NOAA Technical report NMFS'36, U.S. Department of Commerce.
- Kaim-malka, R.A. and S.S. Jacob. – 1985. Données préliminaires sur la biologie de trois espèces de Scorpænidæ de la région de Marseille. *Rapp. P.-V. Réun. Com. Int. Explor. Scient. Mer Méditerr.*, 19 (8): 45-47.
- Kimura, S., Y. Tsukamoto and K. Mori. – 1989. Early developmental stages of the scorpaenid fish, *Scorpaena miodstoma*, reared in the laboratory. *Jpn. J. Ichthyol.*, 35(4): 434-439.
- Love, M.J., B. Axell, P. Morris, R. Collins and A. Brooks. – 1987. Life history and fishery of the California scorpionfish, *Scorpaena guttata*, within the southern California Bight. *Fish. Bull.*, 85(1): 99-116.
- Lowerre-Barbieri, S.K. and L.R. Barbieri. – 1993. A new method of oocyte separation and preservation for fish reproduction studies. *Fish. Bull.*, 91: 165-170.
- Muñoz, M., M. Casadevall and S. Bonet. – 1996. Primeres dades sobre la reproducció de *Scorpaena notata* (Pisces, Teleostei) en el Mediterrani occidental. *Scientia gerundensis*, 22: 53-58.
- Muñoz, M. – 2001. Biologie de la reproduction de quelques Scorpænidæ de Méditerranée occidentale (Teleostei). *Cybium*, 25 (4): 393-394.
- Muñoz, M. and M. Casadevall. – 2002. Reproductive indices and fecundity of *Helicolenus dactylopterus dactylopterus* (Teleostei, Scorpænidæ) in the Catalan Sea (Western Mediterranean). *J. Mar. Biol. Assoc. U.K.*, 82: 995-1000.
- Muñoz, M., M. Casadevall and S. Bonet. – 2002a. The ovarian morphology of *Scorpaena notata* (Teleostei: Scorpænidæ) shows a specialized mode of oviparity. *J. Fish Biol.*, 61(4): 877-887.
- Muñoz, M., M. Casadevall and S. Bonet. – 2002b. Testicular structure and semicyclic spermatogenesis in a specialized oviparous species: *Scorpaena notata* (Pisces, Scorpænidæ). *Acta Zool. (Stockholm)*, 83: 213-219.
- Muñoz, M., M. Sàbat, S. Mallol and M. Casadevall. – 2002c. Gonadal structure and gametogenesis of *Trigla lyra* (Pisces, Triglidae). *Zool. Stud.*, 41(4): 412-420.
- Shchepkin, V.Y. – 1971. Dynamics of lipid composition of the scorpionfish (*Scorpaena porcus* L.) in connection with maturation and spawning. *J. Ichthyol.*, 11: 262-267.
- Siblot-Bouteflika, D. – 1976. *Contribution à l'étude des Scorpænidæ de la région d'Alger*. Ph. D. Thesis, Univ. Aix-Marseille II.
- Simpson, J. – 1951. The fecundity of the plaice. *Fish Invest. London*, 17: 1-27.
- Sokal, R.R. and F.J. Rohlf. – 1995. *Biometry. The principles and practice of statistics in biological research* (3rd ed.) W.H. Freeman and Co., New York.
- Spartà, A. – 1956. Uova, larva e stadi giovanili di Teleostei. Fauna e Flora del Golfo de Napoli. *Monogr.*, 38: 599-626.
- Wallace, R.A. and K. Selman. – 1981. Cellular and dinamic aspects of oocyte growth in teleosts. *Amer. Zool.*, 21: 325-343.
- West, G. – 1990. Methods of assessing ovarian development in fishes: a review. *Aust. J. Marine Freshwater Res.*, 41: 199-222.
- Whitehead, P.J.P., M.L. Bauchot, J.C. Hureau, J. Nielsen and E. Tortonese. – 1986. *Fishes of the North-eastern Atlantic and the Mediterranean*. 1473 p. UNESCO, Paris.
- Wootton, R.J. – 1979. Energy costs of egg production and environmental determinants of fecundity in teleost fishes. In: P.J. Miller (ed.), *Fish Phenology: anabolic adaptiveness in teleosts*, pp. 133-159. Symp. Zool. Soc. London, 44.
- Wourms, J.P. and J. Lombardi. – 1992. Reflections on the evolution of piscine viviparity. *Amer. Zool.*, 32: 276-293.

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