J. Mar. Biol. Ass. U.K. (2005), **85**, 1155–1161
Printed in the United Kingdom

Sexual maturity, fecundity and embryonic development of the spiny dogfish, *Squalus acanthias*, in the eastern Mediterranean Sea

Archontia Chatzispyrou and Persefoni Megalofonou*

Department of Biology, Section of Zoology–Marine Biology, University of Athens, Panepistimiopolis, Ilisia, 15784, Athens, Greece.
*Corresponding author, e-mail: p.megalo@biol.uoa.gr

The reproductive biology of the spiny dogfish, *Squalus acanthias*, was investigated throughout a year, in the eastern Mediterranean Sea. One hundred and eighty specimens were sampled of which 119 were females and 61 males, ranging from 320 to 755 mm and from 350 to 820 mm total length (TL), respectively. The minimum size of mature females was 515 mm and 470 mm TL for mature males (smaller compared with sizes in other studies). Gonadosomatic index (GSI) and hepatosomatic index (HSI) were higher during June and August in female dogfish, respectively; in males GSI had a peak in July and HSI showed its highest value in April. A total of 39 gravid females was identified with TL ranging between 570 and 755 mm. Only 28 of them were bearing embryos; candled uteri were observed in the 11 other gravid animals. A positive relationship was recorded between maternal length and litter size. Ovarian fecundity ranged between 1 and 6 (mean 2.1 ±1.1); uterine fecundity ranged from 1 to 6 (mean 3.3 ±1.2). The size of the pups varied from 72 to 220 mm TL and their weight ranged between 1.6–48.5 g (mean 11.7 ±8.6). The spiny dogfish was compared with fish from other study areas and was found to be smaller in size in the eastern Mediterranean Sea, reaching maturity at smaller sizes and obtaining lower fecundity than female fish in other areas.

INTRODUCTION

Elasmobranchs exhibit complex and diverse reproductive systems and resemble mostly the amphibians and amniotes, rather than the teleosts (Wourms, 1977). Studies on the biology of sharks are limited in comparison with other vertebrates, mainly due to sampling problems. There is relatively little information about the landings of the species and the concern for the inshore fisheries of sharks has increased only recently. The most well studied elasmobranch species are the inshore ones, including the very common and popular spiny dogfish, *Squalus acanthias* L., of the Family Squalidae (Cortes, 2000; Jones & Ugland, 2001; Alonso et al., 2002; Henderson et al., 2002; Shepherd et al., 2002; Soldat, 2002, in the Atlantic Ocean; Ketchen, 1972, 1975; Beamish & McFarlane, 1985; McFarlane & Beamish, 1987; Saunders & McFarlane, 1993; McFarlane & King, 2003, in the Pacific Ocean; Avsar, 2001, in the Black Sea).

The spiny dogfish has a worldwide distribution except for the tropical and polar regions (Compagno, 1984). It is reported to reach 160 cm in total length (TL) and 9100 g weight. Mating takes place once every two years, females exhibiting a biennial cycle and males an annual cycle. *Squalus acanthias* is an ovoviviparous species, where the embryos develop inside the uteri of their mother, in the absence of placenta (Wourms, 1977). The gestation period that lasts almost 2 y (up to 24 months) is the longest ever reported in all shark species (Ketchen, 1972; Nammack et al., 1985). Despite the knowledge obtained from the extensive studies on the species, limited information exists from the Atlantic (Jones & Ugland, 2001; Henderson at al., 2002) and Pacific Oceans (Ketchen, 1972) on the reproduction of the species, and no information from the Mediterranean Sea.

The aim of this study is to provide some basic biological information concerning the reproduction of spiny dogfish from the eastern Mediterranean Sea and to compare the data with that available from other areas. The focus of the study is on the minimum size at first sexual maturity, the fecundity of female dogfish and the embryonic development of the species. Embryonic length is investigated for individual months and the relationship between maternal length and litter size is estimated. Two biological indices (gonadosomatic index [GSI] and hepatosomatic index [HSI]) are examined to test how they are modified during the year and the reproductive cycle.

MATERIALS AND METHODS

Sampling and measurements

A total of 180 spiny dogfish was obtained from the incidental catches of bottom long line vessels and bottom trawlers, between June 2003 and June 2004 (Table 1). Sampling was carried out in the Cyclades and the west and south area of Crete in depths from 350 to 418 m (Figure 1). All specimens used for the purposes of this study were initially preserved in ice (on board) and later frozen at $-20°C$, until dissection.

Spiny dogfish were observed for external damages and wounds, broken spines and torn fins. Total length of each specimen was measured to the nearest centimetre, from the tip of the snout to the tip of the upper lobe of the

Table 1. *Number of specimens and length range (total length [TL] in mm) for male and female spiny dogfish,* Squalus acanthias*, sampled each month from the eastern Mediterranean Sea.*

Month	Sex	Number of specimens	Range of TL
June 2003	m	8	450–760
	f	12	480–680
July 2003	m	3	560–590
	f	10	560–680
August 2003	m	0	
	f	22	545–710
October 2003	m	1	500–500
	f	7	570–660
January 2004	m	23	350–820
	f	19	320–445
February 2004	m	5	500–575
	f	3	480–670
April 2004	m	9	495–525
	f	10	510–710
May 2004	m	6	500–550
	f	21	505–710
June 2004	m	6	510–560
	f	14	550–755

m, male; f, female.

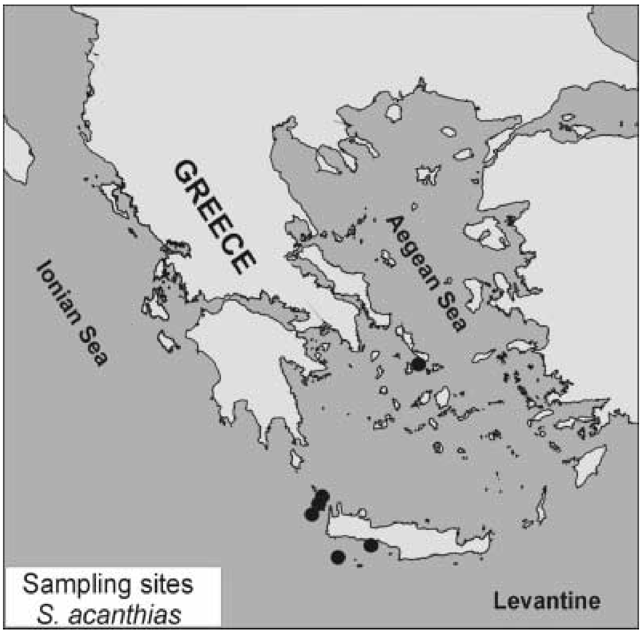

Figure 1. Location of sites (●) at which spiny dogfish, *Squalus acanthias*, was sampled in the eastern Mediterranean Sea.

caudal fin. Round weight (RW) was measured as the total weight of the specimens (animals bearing all internal organs) and was recorded to the nearest gram. Dressed weight (DW) was measured as the weight of the dogfish after the removal of the organs, apart from the heart and the gills, and was recorded to the nearest gram. The Kolmogorov–Smirnov two-sample test was used to test for significant differences in the length and weight frequencies by sex. Linear regression was used to determine length–weight relationships. Differences between sexes were measured with tests of homogeneity of slopes and intercepts. The hypothesis of isometric growth (Ricker, 1975) was tested with a *t*-test.

Sex was determined by direct examination of the claspers of males with the naked eye and claspers were measured to the nearest millimetre. Sex ratios were compared with the 1:1 proportion using the chi-squared test.

Liver and gonads were removed from the body cavity, along with the expanded uteri in the case of gravid females. The length and the weight of the organs were measured to the nearest millimetre and centigram respectively, and examined for parasites or any kind of malformation. Both the GSI and HSI were calculated to examine how they fluctuate during the year and the reproductive cycle using the following formulae:

$$HSI = (LW/DW) \times 100 \quad (1)$$

$$GSI = (GW/DW) \times 100 \quad (2)$$

where GW is gonad weight in g, LW is liver weight in g, and DW is dressed weight of fish in g. The analysis of variance (ANOVA) test was used to test for significant differences in mean GSI values by month, for the sexes separately. The same test was applied for HSI mean values, as well.

Embryonic development

Special attention was given to females with identifiable offspring in their uteri. In the event of a gravid female, embryos were counted, sexed (when possible), measured for TL (to the nearest millimetre), and total weight (to the nearest centigram). The ANOVA test was used for significant differences among the means of embryonic length by month. Moreover, a multiple comparison procedure and a Fisher's least significant difference (LSD) procedure were applied to determine which means are significantly different from which others.

Sex ratio and length–weight relationship were determined. Finally, the developmental stage of all embryos was recorded, based on the size of the external yolk sac (when present) and the morphology of the pups (well developed fins, claspers, eyes etc.). The stages used for the foetuses were based on Jones' study (2001) and divided as follows: Stage 1 (candled embryos)—fertilized eggs in the uteri surrounded by a protective capsule (unsegmented candle); Stage 2 (free-living embryos)—candle has erupted and very small embryos are observed with large yolk sacs, free in the uteri; and Stage 3 (full term embryos)—fully developed embryos present in the uteri, the yolk sac has been absorbed and the umbilical slit is more or less closed.

Fecundity

Fecundity assessment was conducted for mature female sharks. Both ovarian and uterine fecundity were estimated. Uterine fecundity was determined from the number of embryos occupying the uteri, whereas the number of ripe oocytes in the ovaries determined the ovarian fecundity. Oocyte stage was identified macroscopically according to its size and colour. Three stages of ovarian maturity were noted: I, immature (white colour

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ova)—ovum diameter measured less than a millimetre; II, maturing (white-yellow colour)—where ovum diameter ranged between 1 and 20 mm; and III, mature (yellow colour, yolky)—ovum diameter measured greater than 20 mm in length.

When ovaries were large and contained ripe oocytes, ready to be ovulated and all about the same size, they were counted and recorded separately for each ovary (right or left). In addition, the diameters of randomly chosen oocytes of smaller sizes (Stage II) were measured to the lowest millimetre. These diameters were recorded along with the ovary from which the measurements were taken (left or right). Comparisons of ripe oocyte diameter and weight between ovaries were made using a *t*-test.

Maturity stages

Sexual maturity in males was determined by the amount of sperm stored in the testes/epididymis/sperm sac, and by clasper length and rigidity. Males were divided into the following three maturity stages: Immature—sperm not visible in the ducts and testes; uncoiled epididymis and thread like sperm sacs; claspers soft and small; Maturing—testes enlarged; sperm ducts starting to meander; clasper length extends from the fins; and Mature—testes enlarged; sperm sacs well filled with sperm; sperm ducts tightly coiled; claspers stiff and calcified, bearing sharp hooks.

Sexual maturity in females was determined from the size of the ovarian ova and the state of the uteri. Females bearing small oocytes and thread like uteri, were classified as immature (IM). All other females were classified as mature (M) and were divided into six further stages of a continuous reproductive cycle: M(I), non-gravid females with developing ova and expanded uteri; M(II), non-gravid females with ripe ova and expanded uteri; M(III), post-ovulatory females with only fertilized ova in the uteri (candles); M(IV), gravid females with developing embryos that bear external yolk sac; M(V), gravid females with near-term embryos that have absorbed the external yolk sac; and M(VI), post-natal females bearing small ovarian ova and flaccid uteri.

RESULTS

Sex ratio and length–weight relationships

A total of 180 (119 females and 61 males) spiny dogfish was sexed. Overall females outnumbered males by a sex ratio females/males almost 1:0.51, which was significantly different from a 1:1 sex ratio (χ^2-test, $P<0.05$). The range of TL was from 320 to 755 mm (mean=571.2 ±101.4) for females and from 350 to 820 mm (mean=500 ±84.2) for males (Figure 2A). Round weight was found to vary between 125 and 2150 g (mean=916 ±84.2) in female dogfish and between 175 and 2550 g (mean=566 ±342.1) in males (Figure 2B). The results obtained from the Kolmogorov–Smirnov two-sample test indicated that males and females have significantly different length and weight frequency distributions (Kolmogorov–Smirnov test, $P<0.05$).

A positive relationship was found between TL and RW, in both males (R^2=0.98) and females (R^2=0.97) (Figure 3).

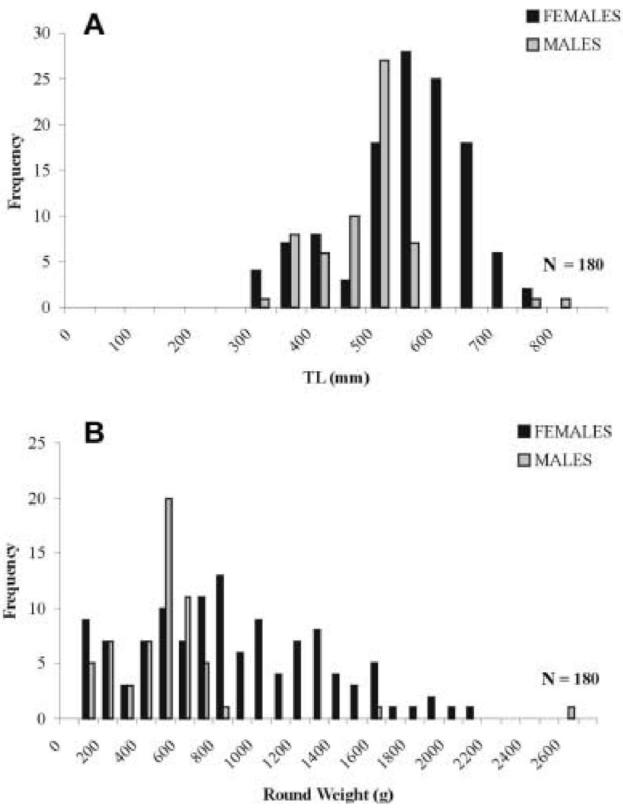

Figure 2. (A) Length and (B) weight distribution of the spiny dogfish, *Squalus acanthias*, in the eastern Mediterranean Sea.

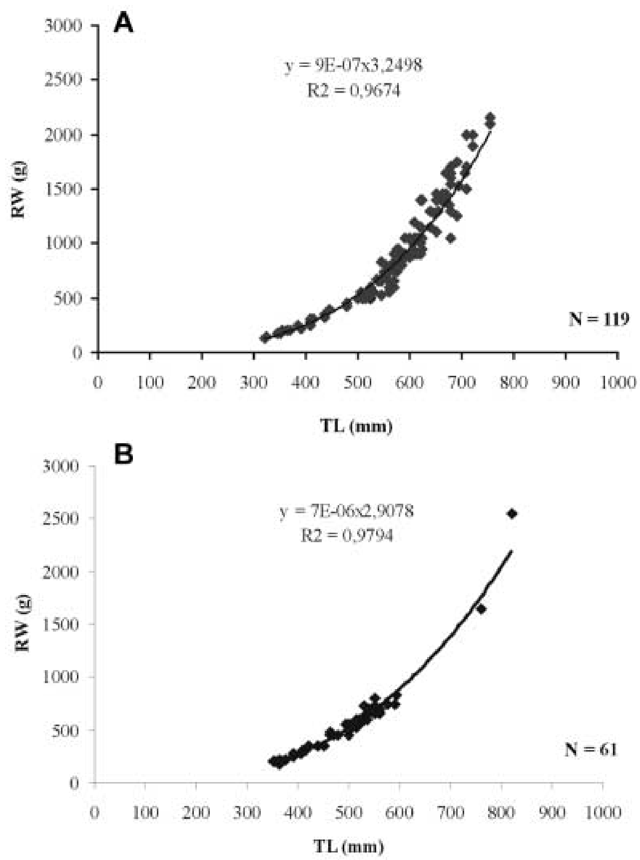

Figure 3. Total length against round weight in (A) female and (B) male spiny dogfish, *Squalus acanthias*, sampled in the eastern Mediterranean Sea.

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The equations of the fitted linear regression model were:

$$\log(\mathrm{RW}) = -13.926 + 3.25 \times \log(\mathrm{TL}) \quad (3)$$

for females and,

$$\log(\mathrm{RW}) = -11.814 + 2.91 \times \log(\mathrm{TL}) \quad (4)$$

for males.

The relationship of TL–RW between sexes was found to be significantly different; there were statistically significant differences among the slopes (ANOVA: P=0.0004) for the various values of sex at the 99% confidence level but there were not statistically significant differences among the intercepts (ANOVA: P=0.2355).

Reproduction of male Squalus acanthias

Gonad weight (GW) in conjunction with clasper length (CL) was a secure indicator of maturity in males. A number of 15 immature, 12 maturing and 34 mature specimens were collected in 8 out of 12 months of sampling.

Testis weight had a positive relationship with TL (Figure 4A). It showed an increase at 470 mm in TL, concurrent with the first mature specimen. Clasper length also increased with TL (Figure 4B) and displayed two distinct groups concurrent with the immature and mature individuals. Smaller sizes of males were bearing claspers smaller than 40 mm; sizes greater than 470 mm had CL greater than 40 mm (Figure 4B). The smallest mature male was found to bear claspers of 49 mm in TL.

Mean hepatosomatic index values per month ranged from 9.7 to 13.4 (mean=12.0 ±1.2), whereas mean GSI values per month varied from 0.7 to 2.1 (mean=1.4 ±0.4). These values in both indices did not show any significant differences between months (ANOVA: $P>0.05$). However, the highest values of HSI were recorded in April (18.7), and lowest in June (3.6), while GSI displayed its highest values in July (3.9) and lowest in January (0.1) (Figure 5A,B).

Reproduction of female Squalus acanthias

A total of 88 females possessing large ovarian eggs and candled or free living embryos in their uteri, was defined as mature. Ovarian weight had a positive relationship with TL (Figure 4C). The HSI monthly mean values varied between 10.4 and 17.3 (mean=13.8 ±2.3) and the respective values of GSI ranged between 0.3 and 5.3 (mean=2.8 ±1.6). The GSI displayed its highest values in June (13.2) and lowest in June and January (0.1) (Figure 5C). The HSI displayed its highest values during August (29.0) and lowest values in May (4.9) (Figure 5D). Both GSI and HSI mean values displayed significant differences between months (ANOVA: $P<0.05$).

Specimens from all mature stages (I–VI) were occupying length-classes of 501–550 mm in TL and reached the highest length-class recorded for female fish (Table 2). All individuals were immature under 505 mm. The smallest mature female measured 505 mm and the largest immature female measured 690 mm (Table 2). The percentages of mature fish in the different length-groups indicate that the length at 50% maturity was about

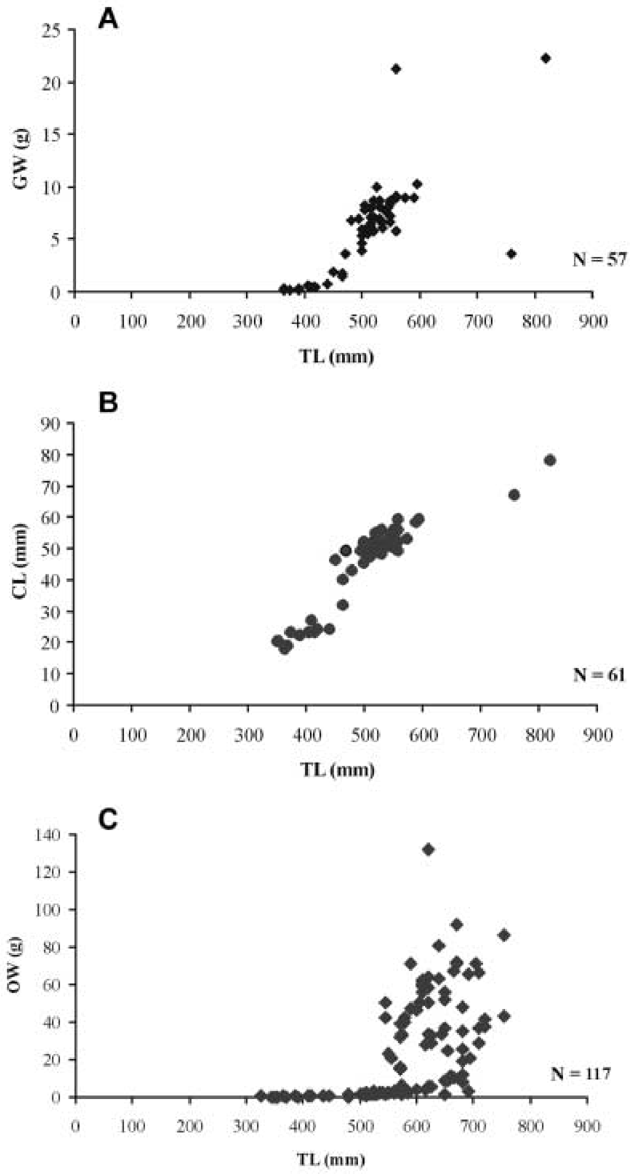

Figure 4. Relationship between total length (TL) and (A) gonad weight; (B) clasper length (CL) recorded from male spiny dogfish; and (C) TL against ovarian weight (OW) recorded from female spiny dogfish, *Squalus acanthias*, sampled in the eastern Mediterranean Sea.

Table 2. *Number of mature and immature female spiny dogfish,* Squalus acanthias*, caught in the eastern Mediterranean Sea by length-class.*

TL (mm)	Number of immature specimens	Number of mature specimens
300–350	4	0
351–400	7	0
401–450	8	0
451–500	3	0
501–550	2	16
551–600	6	22
601–650	0	25
651–700	1	17
701–750	0	6
751–800	0	2

TL, total length.

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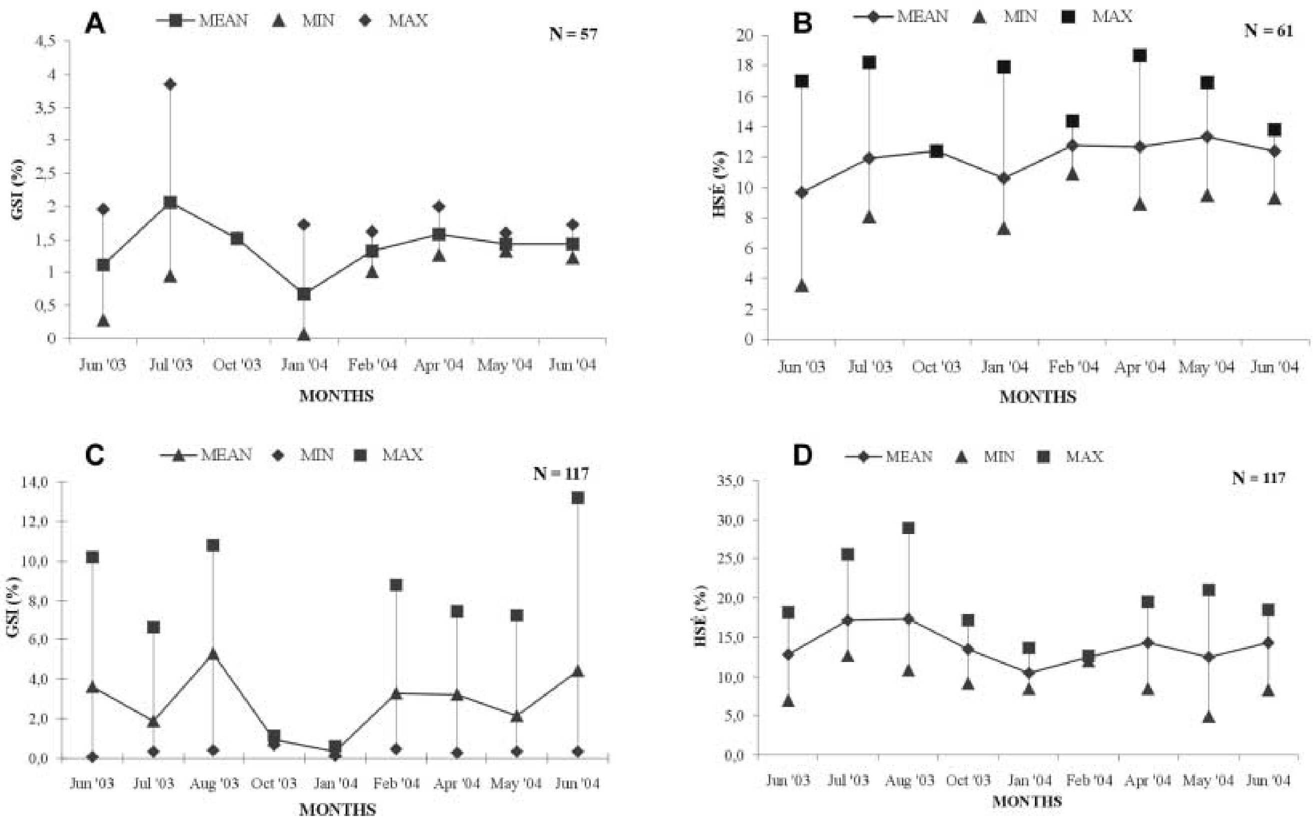

Figure 5. (A) Gonadosomatic index (GSI) and (B) hepatosomatic index (HSI) monthly values of male; (C) GSI and (D) HSI monthly values, obtained from female spiny dogfish, *Squalus acanthias*, sampled in the eastern Mediterranean Sea.

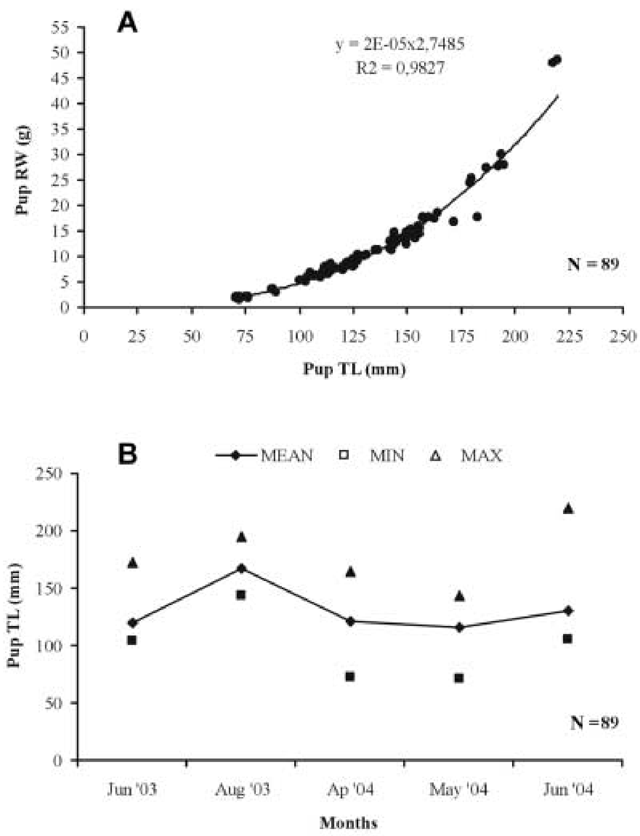

Figure 6. (A) Length–weight relationship of pups; (B) mean embryo total length (TL) per month recorded from female spiny dogfish, *Squalus acanthias*, sampled in the eastern Mediterranean Sea.

518 mm. A total of four animals sampled in July were found to be in Stage VI, indicating that they were in post-natal condition.

Fecundity

Numerous maturing ova (Stage II) occupied the ovaries along with ripe ova. On the left ovary their number ranged from 1 to 22, whilst on the right ovary from 1 to 18. Mature ova (Stage III) showed greater numbers in the left than in the right ovary, too (maximum number recorded=6). The number of ripe ova in individual ovaries ranged from 1 to 6 (mean=2.01 ±1.03) with diameter ranging from 20 to 51 mm (mean=30.1 ±6.1) and of weight between 3.03 and 29.32 g (mean=11.8 ±6.3). Mean ovum weight between ovaries varied significantly (t-test: $t=-2.33$, $P<0.05$); mean ovum diameter though did not show any significant difference between the left and the right ovary (t-test: $t=-1.35$, $P>0.05$).

A total of 89 free-living embryos was found in 28 females, occupying mainly the right rather than the left uterus (1:0.72 ratio). Uterine fecundity ranged from 1 to 6 embryos per female (mean=3.3 ±1.2). In addition, 11 females were recorded to bear candles in their uteri with undeveloped foetuses during May, July and October. Six of them contained segmented candles and five of them non-segmented candles.

Embryonic growth

Embryonic length ranged between 71 and 220 m (mean=131.3 ±33.6) and weight varied from 1.6 to 48.5 g

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(mean=11.7 ±8.6). A positive relationship was recorded (Figure 6A) between TL and RW of pups (R^2=0.98). The sex ratio of female to male pup was 1:0.76, which was significantly different from a 1:1 sex ratio (χ^2-test, $P<0.05$). The highest values of TL were recorded in June and August and the lowest in April and May (Figure 6B), the only months embryos were identified in the oviducts. Only two females had fully-grown embryos (Stage 3), ranging between 183 and 220 mm in TL. Maternal length in these two cases was 620 and 610 mm. The rest of the pups (84 in number) possessed large or moderate-sized yolk sacs (Stage 2).

Mean values of TL varied significantly between months (ANOVA, $P<0.05$). Specifically, specimens from August possessed embryos with highly different TL in comparison with the embryonic TL of the three other months. Candled segmented embryos were recorded in six females (from October and July samples) ranging in number from 2 to 5 (mean=2.8 ±1.2) in both oviducts (Stage 2). A total of five gravid animals (from specimens in May) bore unsegmented candles (Stage 1). Litter size had also a positive linear relationship with maternal length, with a correlation coefficient of 0.38.

DISCUSSION

The present study reports for the first time basic information on the reproductive biology of the species *Squalus acanthias* in the eastern Mediterranean Sea. Our results showed that the spiny dogfish reaches smaller sizes and reproduces at smaller length, in comparison with dogfish from other areas. Previous reports on the maximum size of the spiny dogfish do not coincide with the sizes recorded in the present study. The maximum size recorded in the Atlantic Ocean was 1100 mm (Jones & Ugland, 2001), whereas in the Pacific it was 1300 mm (Saunders & McFarlane, 1993) and in the Black Sea it was 1360 mm (Alonso et al., 2002). Compagno (1984) reported that *Squalus acanthias* grows up to 1600 mm, while Fisher et al. (1987) reported a maximum size of 2000 mm in the Mediterranean Sea. Even though this later value is higher than the ones reported from other areas, it could be attributed to the differences between areas and depths of sampling.

The highest values of fish sampled in the eastern Mediterranean Sea were 820 mm for males and just 755 mm for females. Larger sized fish could not be captured possibly because behavioural factors influence size-distribution and assemblages in different areas. Spiny dogfish is known to be a highly migratory species that swims towards deeper waters as it grows (Jones & Ugland, 2001; Soldat, 2002), or migrates offshore when mating occurs (Fahy, 1989).

Mean length in females was found to be greater than that in males possibly due to the fact that different sizes and sex occupy different depths of the water column. This also might explain the fact that the number of female dogfish was almost twice the number of males.

Size at first maturity was recorded (470 mm for males and 518 mm for females). The lowest maturity sizes that have ever been reported in the Atlantic Ocean are 550 mm for males (Henderson et al., 2002) and 665 mm for females (Alonso et al., 2002). In the Pacific, male maturity is reached at 700 mm and female maturity at 760 mm (Ketchen, 1972), while in the Black Sea the sizes are 670 and 720 mm respectively (Avsar, 2001).

Comparison of TL and RW relationship between sexes during the present study revealed that this relationship is more pronounced in males than in females and the correlation coefficient can confirm this statement (greater in male fish). Females might be growing slower than males due to a great amount of energy lost in pup growth. This is in agreement with the results obtained from the relationship of TL and GW, along with the results from the indices.

Mean values of GSI and HSI did not differ throughout the year for male fish, but this condition did not occur for the opposite sex. Even though HSI in sharks is less variable than it is in teleosts (Henderson et al., 2002), females invest a lot of energy to produce gonadic products. Subsequently the variations in both indices in female dogfish are considered to be a normal situation, as they attain maturity.

Fecundity in the eastern Mediterranean Sea was also lower than that recorded in other seas. It has been reported that developing eggs can measure up to 17 in the ovaries (Jones & Ugland, 2001) and embryos can be as many as 17 in the uteri, of a single female dogfish (Avsar, 2001; Black Sea). The near-term size of foetuses, reported in the Atlantic Ocean, varies between 210 and 280 mm in TL (Alonso et al., 2002). Moreover, Compagno (1984) has reported that litter size varies between 1 and 20 young, the size at birth is 180–300 mm in TL, and the sex ratio is 1:1. Embryos in the present study with fully absorbed yolk sacs measured between 183 and 220 mm in TL, indicating that the size at birth is within the limits reported from the above-mentioned studies. However, sex ratio was found to be different than the 1:1 ratio, between male and female pups; this might be explained by the fact that embryos are aborted when entangled on the nets, due to capture stress (Ketchen, 1972; Henderson et al., 2002).

In the present study the correlation coefficient of maternal length and litter size was 0.38 and a small amount of this variability might be connected with the loss of foetuses during the process of trawling. Ketchen (1972) first suggested these observations, to justify the low r^2 in his preliminary study on *S. acanthias* in British Columbia waters. Therefore, the results from studies on the litter size cannot always be regarded with accuracy as an indicator of minimum fecundity.

In the past the minimum number of candled ova in the oviducts has been used to determine fecundity. In the present study the maximum number of embryos in a single female outnumbered the number of segmented candled eggs in the uteri (6 embryos against 5 candles), possibly due to the limited number of specimens with candled eggs examined. In addition, previous studies have reported that the number of mature ova in the ovaries outnumbered the number of embryos in the uteri (Nammack et al., 1985; Jones & Ugland, 2001), due to the absorption of eggs in the ovaries following fertilization. However, the number of eggs in the ovaries observed in the present study was equal to the number of embryos in the uteri (maximum number recorded in both was 6). Therefore both ovarian and uteri fecundity should be used to describe with safety the fecundity in the spiny dogfish.

The results obtained on the breeding cycle of *S. acanthias* need to be interpreted carefully, since there is no information about the gestation period of the spiny dogfish in the eastern Mediterranean Sea, nor for the parturition–fertilization interval. Therefore no conclusion for the cycle can be deduced with accuracy. However, most authors assume that gestation lasts between 20 and 22 months. Assuming that the maximum diameter of ova in the present study was recorded in May, fertilization must be occurring in spring. Fertilized eggs found to be present in the uteri in May, July and October, are in agreement with the previous statement. Near term embryos from June and August samplings suggest that birth of the pups takes place in the summer. Empty uteri in June may confirm this conclusion.

Overall the present study showed that the spiny dogfish in the eastern Mediterranean Sea reaches smaller sizes than fish in other areas, first maturity is attained at smaller sizes and fecundity is lower than that of gravid females of other areas. In order to describe the reproductive cycle of *S. acanthias* in the eastern Mediterranean Sea, further investigation must take place on the biology of the species by using the first results recorded and presented here.

The authors express their thanks to Mr Dimitris Damalas, PhD student of Biological Oceanography, University of Athens, for his assistance in the sampling.

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Submitted 14 February 2005. Accepted 21 June 2005.