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Seasonality of Reproduction and Embryonic Growth of Spiny Dogfish (*Squalus acanthias* L., 1758) in the Eastern Black Sea

Sefa Ayhan DEMİRHAN[1,*], Kadir SEYHAN[2]
[1]Mustafa Kemal University, Faculty of Fisheries, 31040 Antakya, Hatay - TURKEY
[2]Karadeniz Technical University, Faculty of Marine Sciences, 61530 Trabzon - TURKEY

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Abstract: The seasonality of reproduction and embryonic development of spiny dogfish (*Squalus acanthias*) sampled from the Eastern Black Sea were studied. The gestation period of spiny dogfish, starting in August, September and October, takes around 23-24 months. Fertilized females were caught at a depth of 30-45 m in July and August. Females with full-term pups and empty uteri were found at 50-60 m depth, where the temperature was 10 °C. Lengths of pups at birth were around 28-29 cm, whereas their weights ranged from 68 to 78 g. The models of embryonic growth and development of ova were described as $TL_e = 0.8124 – 0.334 \times mo + 0.1289 \times mo^2 - 0.03 \times mo^3$ (r = 0.92) and $D_o = 0.7364 – 0.1503 \times mo + 0.0221 \times mo^2 - 0.004 \times mo^3$ (r = 0.94), respectively.

Key Words: Reproduction, embryo, *Squalus acanthias*, Black Sea

Doğu Karadeniz'deki Mahmuzlu Camgöz'ün (*Squalus acanthias* L., 1758) Mevsimsel Üreme Döngüsü ve Embriyo Gelişmesi

Özet: Bu çalışmada Doğu Karadeniz'den örneklenen mahmuzlu camgözün (*Squalus acanthias* L. 1758) mevsimsel üreme döngüsü ve embryo gelişimi incelenmiştir. Mahmuzlu camgözün gebelik süresinin Ağustos, Eylül, Ekim aylarında başladığı ve yaklaşık 23-24 ay sürdüğü belirlenmiştir. Çalışmada döllenmiş bireylere 30-45 m derinlikte Haziran-Ağustos aylarında rastlanmıştır. Dölyatakları boş yada dölyataklarında tam gelişmiş embriyo taşıyan dişi bireyler ise sıcaklığın 10 °C olduğu 50-60 m derinliklerde yakalanmıştır. Yavruların yaklaşık olarak 28-29 cm boy ve 68-78 gr ağırlıkta doğdukları tahmin edilmiştir. Embriyo ve yumurta gelişimi ise sırasıyla $TL_e = 0,8124 – 0,334 \times mo + 0,1289 \times mo^2 – 0,03 \times mo^3$ (r = 0,92) ve $D_o = 0,7364 \times 0,1503 \times mo + 0,0221 \times mo^2 – 0,004 \times mo^3$ (r = 0,94) şeklinde kübik fonksyonlarla tanımlanmıştır.

Anahtar Sözcükler: *Squalus acanthias*, üreme, embriyo, Karadeniz

Introduction

The spiny dogfish, *S. acanthias,* is a coastal squalid shark with a circumboreal distribution (Bigelow and Schroeder, 1953) including the Mediterranean and Black Sea (Aksiray, 1987; Compagno, 1989; Avsar, 2001).

Reproduction of *S. acanthias* has been studied extensively in different seas of the world (Ford, 1921; Hickling, 1930; Templeman, 1944; Hisaw and Albert, 1947; Ketchen, 1972; Jones and Geen, 1977; Gauld, 1979; Nammack et al., 1985; Hanchet, 1988). The spiny dogfish is a non-placental viviparous species of Elasmobranchii. Parturition occurs offshore in winter (Bigelow and Schroeder, 1953; Soldat, 1979). Fertilization takes places internally and embryos develop over 22-23 months. Subsequently, a female mates and ovulates a new set of eggs shortly after the birth of the previous pups (Hanchet, 1988). Previous studies were concerned with the taxonomy, growth, food composition and distribution of the species in the Black Sea (Carausu, 1952; Svetevidov, 1952; Slastanenko, 1956; Ionescu and Serpoianu, 1958; Karmanova et al., 1976; Compagno, 1989). No detailed information is available on the reproduction of *S. acanthias* apart from that reported by Avsar (2001), who gave only a brief account.

* E-mail: sademirhan@yahoo.com

The aim of this study was to investigate and gain more information on the seasonality of reproduction and embryonic development of the spiny dogfish, in particular; to determine the duration of gestation; to define the timing and depth at which parturition, mating, and ovulation take place; and to determine average size at birth.

Materials and Methods

Spiny dogfish were caught off Çamburnu, Trabzon, located on the SE Black Sea coast, near the Georgian border (Figure 1). Sampling was performed using longlines at 35-45 m depths in summer and 30-60 m depths in autumn. Spiny dogfish were also sampled from commercial purse seines operated in winter at 25-50 m depths. Some fish were also sampled in spring by longlines at depths of 80-120 m in the same area.

All fish sampled were sexed, measured and their reproductive stages determined according to Templeman (1944), Jones and Geen (1977) and Karatas et al. (2005). The body (W_p) and liver (W_{pl}) were weighed to the nearest 10 g. To estimate the gestation period, average length of the embryo in the uterus of each specimen was plotted according to sampling dates as given in Hanchet (1988).

Embryos longer than 7 cm could be sexed externally. The presence or absence of external and internal yolk sacs was also recorded. The length of all embryos (TL_e) and diameter of eggs (D_o) were measured to the nearest millimeter. The total weight of embryos (W_e), liver weight (W_{le}), external yolk sacs of embryos (W_{ys}), individual weight of eggs (W_o), and total weight of ovaries (W_{to}) were weighed to the nearest 0.01 g. Relationships between liver weight and total weight, liver weight and length, yolk sac weight and total weight, yolk sac weight and length of embryos were established to estimate the length at birth, and their relations to reproductive stages were shown.

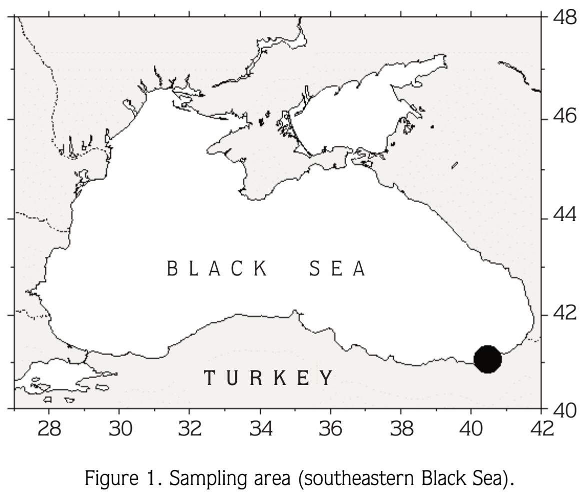

Figure 1. Sampling area (southeastern Black Sea).

The gonadosomatic index (GSI) was calculated following Parameswarn et al. (1974). Liver indexes of parents (LI_p) and embryos (LI_e) were calculated according to the following equation to understand the changes depending on the gestation period.

$$LI_p = (W_{pl}/W_p) \times 100 \text{ and } LI_e = (W_{el}/W_e) \times 100$$

where W_{pl} is liver weight of parents, W_{el} is live weight of embryos, W_p is total weight of parents, and W_e is total weight of embryos.

A nonlinear regression was performed to determine the embryonic growth and development of eggs.

$$TL_e = b_1 - b_2 \times mo + b_3 \times mo^2 - b_4 \times mo^3$$

$$D_o = b_1 - b_2 \times mo + b_3 \times mo^2 - b_4 \times mo^3$$

where TL_e is total length of embryo, D_o is diameter of egg, mo is months old, and b_1, b_2, b_3 and b_4 are constants.

Results

Characteristics of Embryo and Egg

A total of 515 embryos were sexed, of which 264 (51%) were female. The sex ratio was not significantly different from unity ($P > 0.05$). The length frequency of the embryos is given in Figure 2.

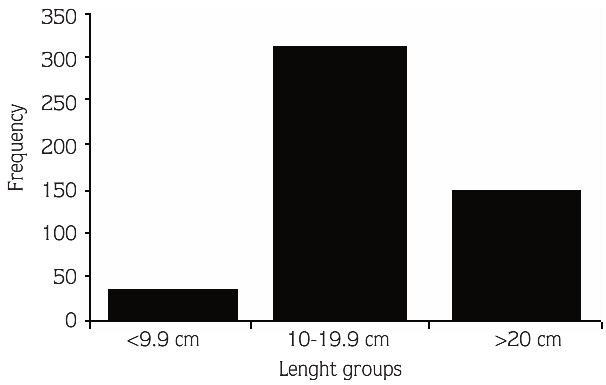

Figure 2. Length frequency of embryos of *S. acanthias* in the southeastern Black Sea in 2000-2003.

The length (TL_e)-weight (W_e) relationship was also studied for all embryos available. Differences were not statistically significant between the sexes or between embryos from the left and right uterus ($P > 0.05$). Therefore, all data were pooled and a common relationship between length and weight in 530 embryos was constructed. The relationship was $W_e = 0.015 \times TL_e^{2.49}$ ($r = 0.99$). The relationship between egg diameter (W_o) and weight (D_o) was also worked out, and it was found that eggs increase in weight exponentially: $W_o = 0.004 \times D_o^{2.33}$ ($r = 0.96$) (Figures 3a, b).

Seasonality of Reproduction

The sexual activity of spiny dogfish is shown in Figure 4. Females at the early candle stage were observed in August and September at depths of 30-45 m with the temperature around 12-15 °C. However, females at the spent stage were caught in August, September and November at 50 m at 9 °C. However, males with empty ampullae were caught in June and July. Meanwhile, females were also observed to be at the early candle stage in August when they were caught at 30-55 m at water temperature 9-17 °C (Figure 5).

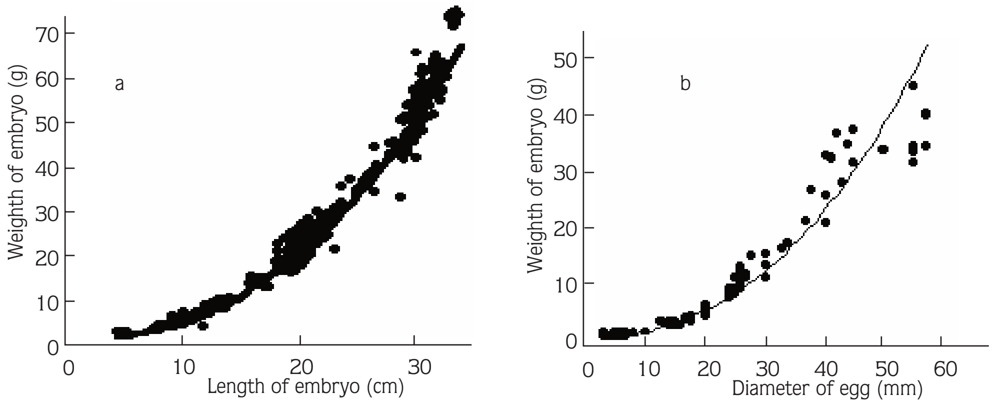

Figure 3. Length-weight relationship of embryos (a) and diameter-weight relationship of ovarian eggs of *S. acanthias* (b).

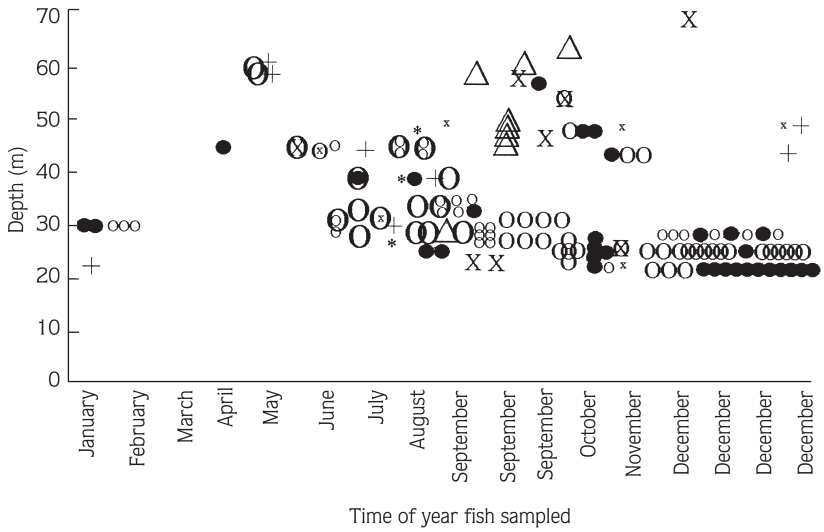

Figure 4. Sexual activities of all specimens sampling over 17 months (x immature male, + immature female, X mature male, * males with empty ampullae ● Candle Stage, o Post-Candle Stage I (embryo size < 10 cm), O Post-Candle Stages II-III (embryo size 10-20 cm), O Full-Term Embryo Stage (embryo size >20 cm), Δ Spent Stage

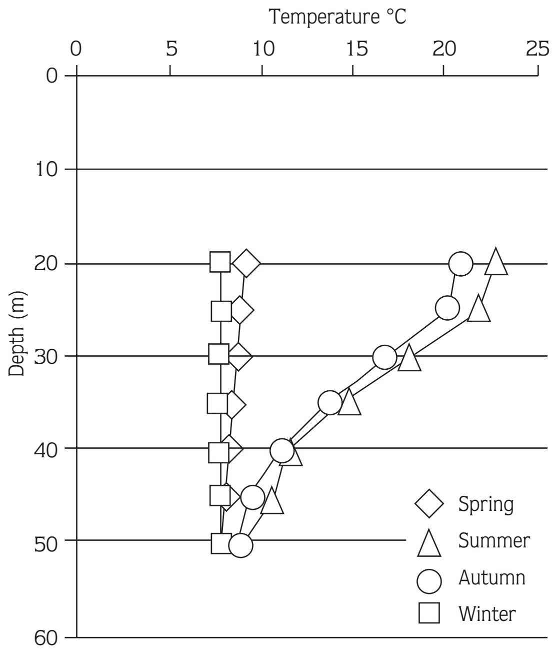

Figure 5. Sea temperature by depth and season.

Proportions of pregnancy stages or sexual activity of specimens caught during the sampling period over 3 years are given in Figure 6. Males had sperm and bruised claspers in July, August and September together with females. However, females with no embryo but with developed eggs in their uteri were found in September and October.

Average embryo length in the uterus of each specimen was plotted against sampling dates to examine the gestation periods of *S. acanthias.* Distributions of embryo lengths at different sampling dates showed a clear linearity (Figure 7).

Development of Embryo and Egg

The growth in length of embryos and diameter of eggs were investigated throughout the pregnancy period and are given in Figure 8. In both cases, growth was best described by a cubic function, but a significant increase in embryo length was observed regarding growth in egg diameter. Moreover, the increase in egg diameter became more apparent when they reached about 10-12 cm.

$TL_e = 0.8124 - 0.334 \times mo + 0.1289 \times mo^2 - 0.03 \times mo^3$ ($r = 0.92$)

$D_o = 0.7364 - 0.1503 \times mo + 0.0221 \times mo^2 - 0.004 \times mo^3$ ($r = 0.94$)

Embryo development was also investigated considering the time of fertilization. The investigation showed that the candles ruptured and caused release when they were 6-7 cm in length with large external yolk sacs into the uterus. The candled embryos stage lasted 6-8 months, from August to February. Free embryos of 6-7 cm, still bearing external gills, were obtained in February, after which adult females were no longer caught in the sampling areas over 2 months. Embryos 10-12 cm in length, in their one year of development

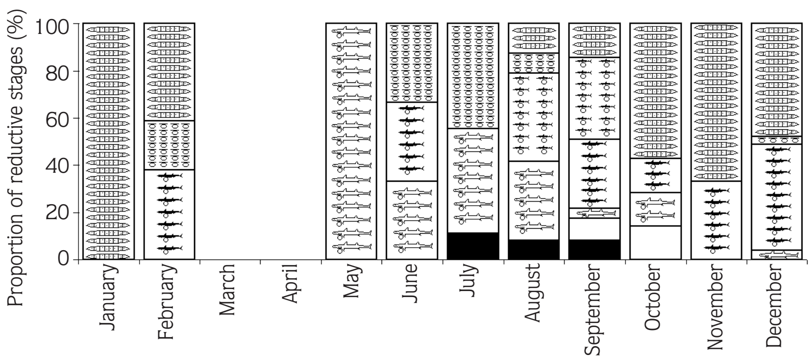

Figure 6. The proportion of females in each of reproductive stages and males over the 2-year cycle (mature male, Candle Stage, Post-Candle Stage I (embryo size < 10 cm), Post-Candle Stage II (embryo size 10-15 cm), Post-Candle Stage III (embryo size 15-20 cm), Full-Term Embryo Stage (embryo size >20 cm), Δ Spent Stage)

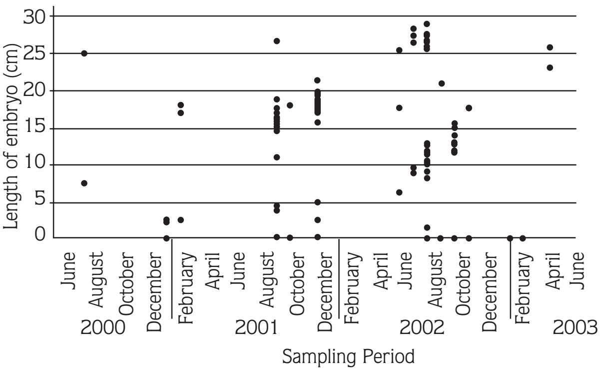

Figure 7. Average length of embryo in the uterus of each specimen sampled.

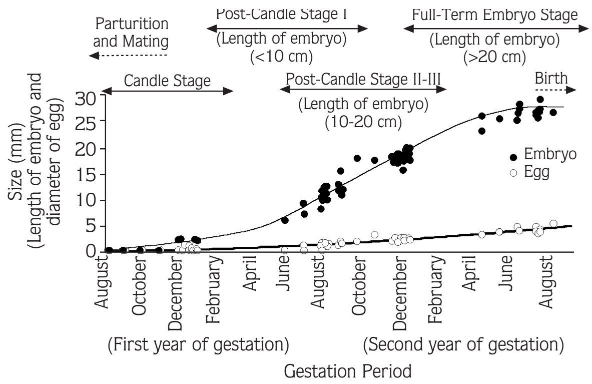

Figure 8. Development of embryo and ovarian eggs in a pregnancy period of *S. acanthias*.

after conception, were present in August and September. Embryos of greater length (25-28 cm), in their second year of development, were caught from July to September, but only in August and September had the external yolk sac been fully absorbed and internal yolk sacs on the intestines were present (Figures 4 and 6).

We looked at the length of embryos soon after becoming available. The data provided for the year classes concerned were promising (Figure 9). Therefore, an attempt was made to compare the embryonic growth for the year classes of 2001, 2002, 2003 and 2004 by plotting the length of embryos (TL_e) against the time of the year sampled. A linear relationship with a high regression coefficient for each was obtained (Table).

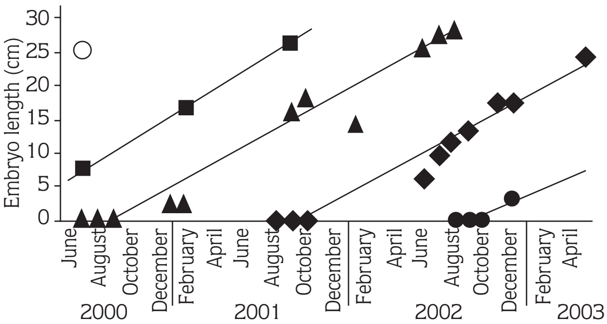

Figure 9. The growth of embryos for different year classes; 2000 year class (fertilization occurred in 1998, birth occurred in 2000), ■ 2001 year class (fertilization occurred in 1999, birth occurred in 2001), ▲ 2002 year class (fertilization occurred in 2000, birth occurred in 2002), ◆ 2003 year class (fertilization occurred in 2001, birth occurred in 2003), ● 2004 year class (fertilization occurred in 2002, birth will occur in 2004)

Differences were not statistically significant between growth of the 2001, 2002 and 2003 year classes ($P > 0.05$). However, growth of the 2004 year class was different from that of the others. The differences were due to the lack of developed embryos in the 2004 year class.

Length of Embryo at Birth

The longest embryo found in the uterus of a specimen (132.5 cm in length) during the sampling period was 29.4 cm. Sixteen embryos with small external yolk sacs belonging to that female were capable of surviving for 2 weeks. Embryos swum in the aquarium freely and absorbed their yolk sacs in the 2 weeks before they died. Observations on the weight of yolk sacs and length and weight of embryos showed that pups at birth were on average 27-28 cm in length and 68-70 g in weight.

Gonadosomatic Index (GSI)

The changes in GSI in spiny dogfish over a gestation period are given in Figure 10. It was lowest at the candle stage, from August to February (0.68%), and highest at the spent stage, from September to November (9.14%). A rapid increase in GSI was also observed after the post-candle stage, when they were about 10-15 cm in length.

Liver Index (LI)

The liver index (LI_p) of females was evaluated within their gestation periods to illustrate the variations. It increased only between post-candle stages II and III from 24.0% to 27.12% during winter (Figure 11). Similarly, liver weights of embryos (LIe) increased simultaneously between these stages (Figure 12a and b). The relationship between embryo length and the weight of the yolk sac was also analyzed. It was found that yolk sac

Table. Embryonic growth of Squalus acanthias in different year classes where TL_e is the total length of embryo, "m" is the month, and "n" is the number of parents.

Date of Fertilization	Birth occurred in (Year Classes)	Model of growth	n	r
1999	2001	TLe = 1.36 × M × 4.71	3	1.00
2000	2002	TLe = 1.35 × M × 3.67	7	0.97
2001	2003	TLe = 1.27 × M × 3.03	10	0.96
2002	2004	TLe = 0.90 × M × 1.60	4	0.77

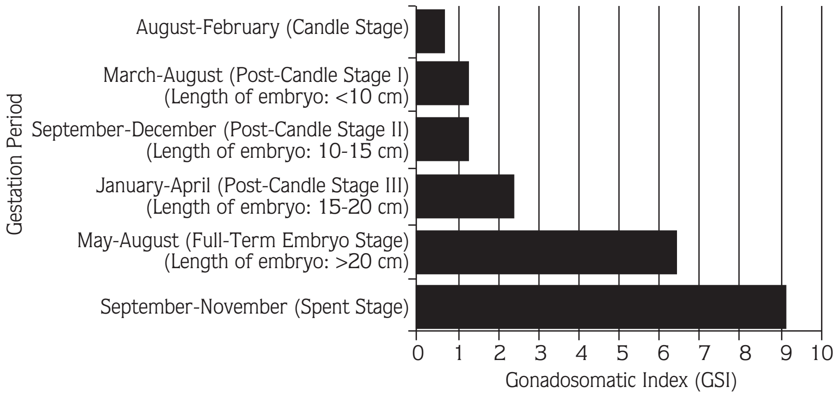

Figure 10. A detailed description of GSI in *S. acanthias* over a pregnancy period in the SE Black Sea.

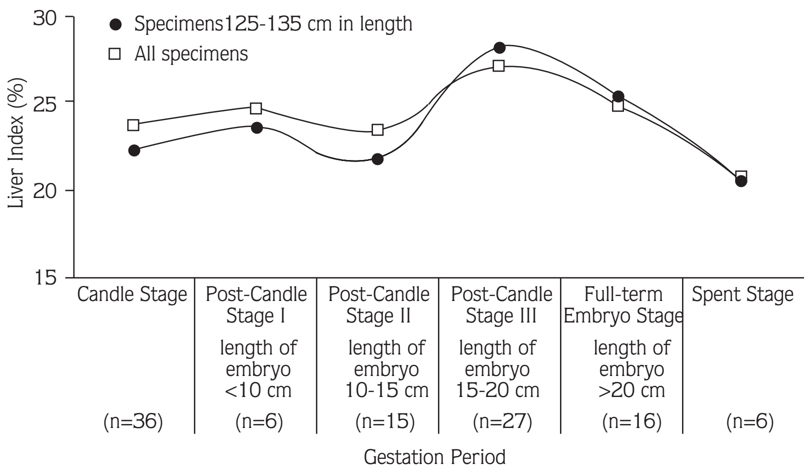

Figure 11. Variation of liver index of *S. acanthias* in pregnancy periods.

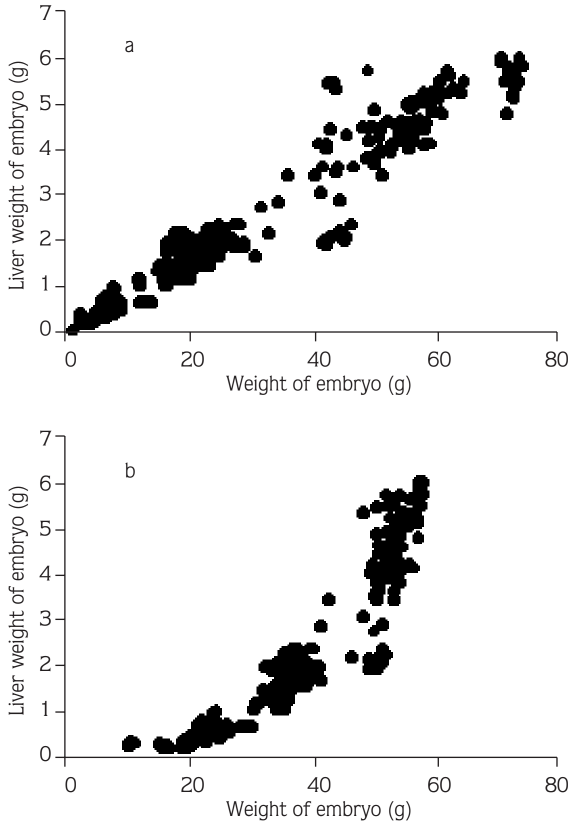

Figure 12. Relationship between liver weight and weight of embryo (a); liver weight and length of embryo (b).

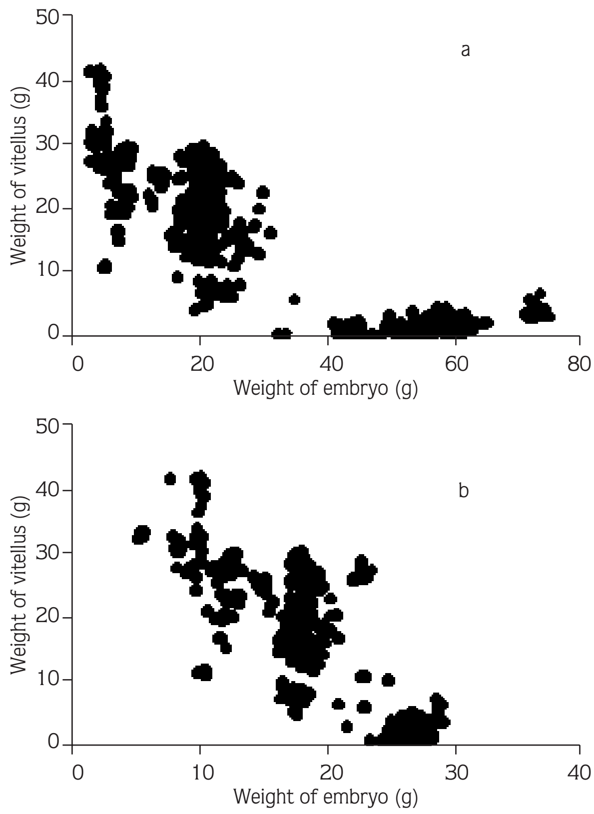

Figure 13. Relationship between weight of vitellus and weight of embryo (a) and between weight of vitellus and length of embryo (b).

weight decreases rapidly as the length of the embryo increases (Figure 13a and b).

Discussion

Spatial Distribution of Specimens

All specimens at all the reproductive stages were caught at 25-60 m depth, which is different from the other populations of spiny dogfish (Hickling, 1930; Holden, 1965; Gauld and MacDonald, 1982; Fahy, 1988; Moore, 1998; McMillan and Morse, 1999). The reason is probably the characteristics of the Black Sea. The Black Sea is the largest anoxic, or oxygen-free, marine system, resulting from the great depth of the sea and the relatively low salinity (and therefore density) of the water flowing into it from rivers and the Mediterranean. Freshwater and seawater mixing is limited to the uppermost 100-150 m, with the water below this interface being exchanged only once every thousand years (Shnjukov et al., 1997). This mix is extremely toxic, resulting in a sea that has almost all of its ecology living in that top layer down to a depth of approximately 150 m, below which there is basically no life at all.

Sample Characteristics

There have been numerous studies on the migration and flock behavior of spiny dogfish (Hickling, 1930; Bigelow and Schroeder, 1953; Holden, 1965; Hjertenes, 1980; Gauld and MacDonald, 1982; Nammack et al, 1985; Ketchen, 1986; Compagno, 1989; Vince, 1991; Steinberg, 1997; Fahy, 1988; McMillian and Morse, 1999; Shepherd, 2002). The behavior of spiny dogfish is affected by sampling carried out by gear using a certain place, depth and season. The gear used can catch a flock consisting of a certain sex or size or those that have embryos in the same developing stages.

The proportion of sexes obtained from this study is not in agreement with the result given by Avsar (2001), who made observations in the Black Sea as well, but it is in agreement with the result given by Sosinski (1978), who found that females were dominant in the sample. Consequently, it can be concluded that the sampling station and period can play an important role in catching the specimens. We think that this is particularly the case for females at different pregnancy stages.

Frequency of Embryos

The frequency of embryos at the candle stage and post-candle stage I (<10 cm) was low because the sampling period comprised the 2002 and 2003 year classes, almost having the whole of these stages, and the 2004 year class, having these stages in part. Post-candle stages II and III in the 10-20 cm length groups had the highest embryo frequency because the sampling period comprised the 2001, 2002 and 2003 year classes.

The frequency of the full-term embryo stage was relatively low. The other reason for the unbalanced distribution of frequency could be the difficulty in catching parents at the candle, post-candle I and full-term embryo stages. These stages occur in spring, when sampling is difficult.

Reproduction

Many researchers have suggested that parturition in spiny dogfish occurs in shallow waters (Templeman, 1944; Holden, 1965), which is also the usual pattern for many other elasmobranches (Springer, 1967). Compagno (1989) stated that spiny dogfish move inshore to mate in April and May in the Black Sea. Our findings are in agreement with his statement, considering sperm storage reported for elasmobranches (Gauld, 1979; Pratt and Tanaka, 1994). Gauld (1979) implies that the short period during which sperm were found, and the low frequency of females carrying sperm suggest that ovulation closely follows mating in about 4 weeks.

Bigelow and Schroeder (1953) and Graham (1956) hypothesized that parturition occurs offshore, whilst Ketchen (1972) found that parturition takes place in mid water. However, Compagno (1989), Hickling (1930) and Templeman (1944) indicated that birth occurs in shallow waters similar to the conclusions reached by Beamish and Smith (1976) and Beamish et al. (1982). Hickling (1930) stated that there is a shoreward migration of pregnant females, as did many other researchers (Bigelow and Schroeder, 1953; Jensen, 1965; Moore, 1998). Probably the best conclusion is that drawn by Compagno (1989) and Wheeler (1969). They stated that shoals of spiny dogfish show irregular movement, although the mature females regularly migrate into shallow waters to give birth. Females at spent stages were caught in deeper waters than others. We caught no fish in March or April. It is thought that they probably migrate during this period.

Seasonality of Reproduction

The seasonality of the reproduction in female spiny dogfish has been reasonably well defined (Ford, 1921; Hickling, 1930; Templeman, 1944; Gauld, 1979; Hanchet, 1988). In our study, on any particular sampling date groups of females carrying different sizes of embryo could usually be identified (see Figures 4 and 6). The pregnancy period of spiny dogfish is quite long and differs from one to the other. Kirnosova (1989) pointed out that the spiny dogfish in the Black Sea needs only 12 months for the gestation process. It is, in the meantime, known that a period of 22-25 months causes spreading of the pregnancy stage over all months of the year (Ford, 1921; Hickling, 1930; Templeman, 1944; Bonham et al., 1949; Holden and Meadows, 1964; Ketchen, 1972; Jones and Geen, 1977; Sosinski, 1978; Gauld, 1979; Slauson et al., 1983; Nammack et al., 1985; Hanchet, 1988; Compagno, 1989) and it makes it harder to understand the pregnancy stages or time (Ford, 1921; Holden and Meadows, 1964; Gauld, 1979; Hanchet, 1988). Females with candled embryos have no developing embryos (early candle stage) and this, along with males with empty ampullae, is a sign of fertilization (beginning of pregnancy) and that mating takes place months before (Gauld, 1979). It was noted that parturition occurs from July to October in the present study. It was also observed that the gestation period, starting in August, September and October, takes around 23-24 months (see Figures 4 and 6).

The seasonal timing of the reproductive stages, and the duration of gestation differ from the findings of Templeman (1944), Ketchen (1972), Nammack et al. (1985), Jensen (1965) and Holden and Meadows (1964). They stated that parturition and ovulation occur between October and January mainly, which slightly differ from the current study.

Length and weight of embryos at birth estimated from the relationship between yolk sac weight-embryo weight, embryo length-embryo weight and observations (27-28 cm and 68-70 g) were similar to the values stated for other spiny dogfish populations (Ford, 1921, Hickling, 1930; Kaganovskaia, 1937; Templeman, 1944; Yamamoto and Kibezaki, 1958; Aasen, 1964; Ketchen, 1972; Bass et al., 1976; Jones and Geen, 1977; Sosinski, 1978; Gauld, 1979; Slauson et al., 1983; Nammack et al., 1985; Hanchet, 1988; Compagno, 1989; McMillian and Morse, 1999). Birth length of embryos estimated from the von Bertalanffy growth equation was smaller (19 cm) than our observations. The reason for this might have been that the VBGE does not reflect the early life of spiny dogfish as given in Holden (1977).

We observed that ovarian egg growth occurs simultaneously with embryo growth, but it became apparent when they reached about 10 to 12 cm. The same observation was also reported by Nammack et al. (1985) (see Figure 8).

Gonadosomatic Index and Liver Index

Liver indexes of females were estimated through gestation periods to evaluate the variation. It increased between post-candle stages II and III from 24.0% to 27.12% during winter (see Figure 11). GSI also started to increase during the same period, but slowed down to the end of post-candle stage II (see Figure 10). Similarly, the liver weight of embryos also increased, but yolk sac weight of embryos decreased at post-candle stages II and III (see Figures 12a, b and 13a, b). It was observed that the liver indexes estimated decreased rapidly between post-candles stage III and the spent stage. It was at the lowest level (20.82%) for pregnant females. The decrease in liver weight during this period might be a sign that it is spent for the energy requirement for the growing of embryos as Amesbury (1997) stated. In this study, a rapid decrease in the liver index in the winter was also observed and was at its lowest level (20.82%) in bearded females. This is probably due to voraciously feeding on anchovy in the area.

Conclusions

The gestation period of spiny dogfish, starting in August, September and October, takes around 23-24 months. Ovarian egg growth occurs simultaneously with embryo growth, but it became apparent when they reached about 10 to 12 cm. Liver indexes of females increased between post-candle stages II and III during winter. Moreover, GSI also starts to increase in the same period, but slows down to the end of post-candle stage II. Similarly, the liver weight of embryos also increased, but yolk sac weight of embryos decreased at post-candle stages II and III. Liver indexes decreased rapidly between post-candle stage III and the spent stage and it was at the lowest level for pregnant females. The decrease in liver weight during this period might be a sign that it is spent for the energy requirement for the growing of embryos.

Legends:

D_o, Diameter of eggs

GSI, Gonadosomatic index

LI_e, Liver index of embryo

LI_p, Liver index of parents

Mo, Age of embryo (monthly)

TL_e, Total length of embryo

TL_p, Total lengths of parents

W_e, Total weight of embryo

W_{le}, Liver weight of embryos

W_o, Individual weight of eggs

W_p, Total weight of spiny dogfish

W_{pl}, Liver weight of spiny dogfish

W_{to}, Total weight of ovarian

W_{ys}, Weight of external yolk sacs of embryos

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