Reproduction of female spiny dogfish, *Squalus acanthias*, in the Oslofjord

Thomas S. Jones
Hans Oeverlandsvei 10
1363 Hoevik, Norway
E-mail address: tomtrussel@hotmail.com

Karl I. Ugland
Department of Biology
University of Oslo, Pb. 1064
0316 Oslo, Norway

The spiny dogfish (*Squalus acanthias*) is a relatively small shark with a characteristic spine in front of each dorsal fin. Its dorsal side is grayish and has sporadic white spots. Although it may reach a length of 160 cm, most individuals in the North Sea are in the range of 80–100 cm (Ford, 1921). It is distributed worldwide, absent only from tropical and polar regions (Compagno, 1984).

The spiny dogfish has been harvested for more than 100 years mostly for its oil-rich liver (Ketchen, 1986). At first, the oil was used for lamp fuel and as a lubricant in machines. The oil was later (during W.W.II) used as a source of vitamin A. Today the dogfish is valued as food in many countries (Gordon, 1986).

The reproduction cycle of the spiny dogfish begins with mature females bearing several large (over 40-mm) yellow eggs. As the eggs pass through the shell gland they are fertilized and become enclosed in a protective capsule (candle). The candle passes down the reproductive tract and comes to rest in the uterus. The embryos live off the large yolk sac attached under the gill region (Gilbert, 1981). As the embryos grow, they slowly absorb the yolk sack. Embryos that have completely absorbed the yolk sac may still remain in the uterus for some time before being born (Ford, 1921). According to Jones and Geen (1977), the embryos also bear an internal yolk sac which nourishes them for up to 2 months after birth. The dogfish reproductive cycle takes almost 2 years, one of the longest gestation periods of any living vertebrate (up to 24 months) (Ketchen, 1972; Nammack et al., 1985).

This shark, like other sharks, is very susceptible to overfishing, not only because of its long gestation period, but also because of slow growth, late maturity, and because it bears a small number of offspring (up to 15) (Nammack et al., 1985; Fahy, 1989). Extensive fishing since the early 1960s has led to a marked decrease in the North Sea stock. Fishing has also affected the population in the Oslofjord where the annual catch declined from 704 tons in 1979 to less than 300 tons per year during the 1990s (Official Statistics of Norway, 1996). We investigated dogfish reproduction in the Oslofjord by comparing the reproduction parameters of dogfish caught in 1987 and 1997. The focus of our study was to evaluate the reproductive parameters of spiny dogfish in the Oslofjord and to look for possible changes in these parameters.

Materials and methods

Sampling

Dogfish were sampled monthly off the Hvaler Islands throughout 1987 and 1997 in gill nets and by longline at depths ranging from 50 to 460 m (Fig. 1). The gill nets were composed of monofilament line (0.60 mm) with a mesh size of 285 mm. This large mesh size accounts for catches consisting mainly of larger dogfish (over 70 cm). The longline was composed of a 5-mm line connected to a 7/0 dogfish hook. The nets were usually checked every 24 hours while the longline was taken up after a few hours. The samples consisted of 132 females in 1987 and 101 females in 1997. Total length and weight were measured to the nearest 0.5 cm and 5 g, respectively, as described by Saunders and McFarlane (1993).

The same fisherman, fishing grounds and fishing gear were used in both sampling years, so that sampling bias was avoided. The fishing gear accounted for catches of dogfish that were mainly over 70 cm in length. There was a relatively small amount of unmarketable-size fish caught and the discard rates were approximately the same in both years.

Age determination

The first and second dorsal spines were removed from 217 dogfish. The remaining 16 dogfish had spines that were either missing, or broken to such an extent that age determination was not possible for these individuals. The spines were air-dried at least 1 week before being cooked for approximately 3 minutes each in tap water. The flesh around the base of the spine was then removed with a scalpel and tweezers. The cleaned spines were subsequently dipped in ethyl alcohol and then dried with a soft cloth. Next, the spines were viewed under an Olympus SZH 10 zoom stereo microscope and aged according to the method described by Ketchen (1975). For large individuals with worn spines, age was modified by Ketchen's (1975) correction curve for age

$$Y = 0.5097X^{2.55},$$

where X = the diameter of the spine base in millimeters; and
Y = the additional age of the spine due to it being worn.

Ketchen's correction curve is based on fish caught in the Strait of Georgia, British Colombia. It is quite likely that there are differences in juvenile growth in the respective dogfish populations. The result may therefore be bi-

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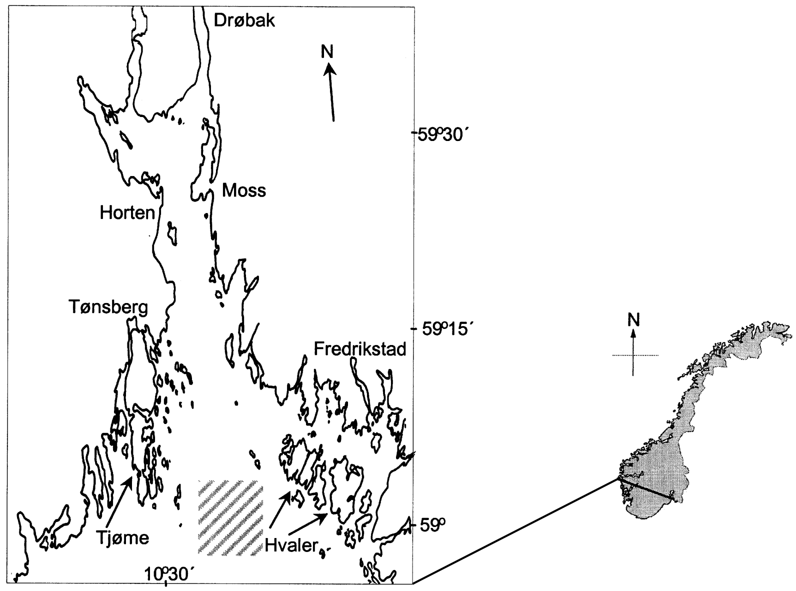

Figure 1

Map of the Oslofjord. The gray shaded area represents the capture location of dogfish in the outer Oslofjord.

ased and in future work a correction curve will have to be made for the stock in the Oslofjord.

Embryo development

Both ovaries of mature females were rinsed to expose eggs. The rinsing process consisted of removing and then carefully opening the ovaries with a scalpel. The eggs were counted and registered as belonging to the right or left ovary. In pregnant females the embryos were counted and sexed. The embryos were then measured to the nearest 0.1 cm on millimeter paper. Three stages of embryo development were identified according to Gauld[1]: stage 1 (candled embryos)—eggs, apparently fertilized, are present in a protective capsule in the uteri; stage 2 (free-living embryos)—the candle has ruptured and embryos bearing an external yolk sac are free in the uteri; and stage 3 (full term embryos)—fully developed embryos are present in the uteri. The yolk sac is fully absorbed and the umbilical slit is more or less closed.

Results

Biological parameters

The fish ranged in length from 54 to 110 cm in 1987 (mean 87 cm) and from 68 to 108 cm (mean 88 cm) in 1997. Weights ranged from 0.4 to 5.7 kg (mean 2.6 kg) in 1987 and from 1.1 to 5.5 kg (mean 2.9 kg) in 1997. Ages ranged from 9 to 35 years (mean 25 years) in 1987 and from 10 to 38 years (mean 23 years) in 1997.

On average, the fish in 1987 were 1.8 cm longer than fish in 1997 at the same age (P=0.02). However, there was a large variation in the length, and age could only account for 38% of this variability. Length accounted for 76% of the variability of the weight in 1987 and 93% in 1997. Fish between 80 and 110 cm were about 500 g heavier in 1997 (P<0.01). This difference was reflected in the condition factor, which was 3.8 in 1987 compared with 4.2 in 1997. This indicates that female dogfish caught in 1987 were longer and lighter than in 1997.

Growth

Growth appeared to be best represented by a linear growth equation for dogfish between the ages of 11 and 38 years, with an average annual increment of 0.7 cm per year (Fig. 2). There was no sign of reduction in growth with increasing age; that is, no asymptote was detected in these data.

Age and length at maturity

Maturity was defined as females bearing large ovarian eggs with a diameter of over 2 cm, candled young or free-living embryos. In both 1987 and 1997, most of the females matured between 12 and 26 years of age. PROBIT analysis indicated that dogfish reached 50% maturity at an age of 17.6 years in 1987 and 17.0 years in 1997 (Fig. 3). The

[1] Gauld, J. 1979. Reproduction and fecundity of the Scottish-Norwegian stock of spurdogs, *Squalus acanthias* (L.). ICES, Council Meeting (CM) 1979/H:54, 13 p. Directory of fisheries, biblioteket, Pb. 185, 5001 Bergen.

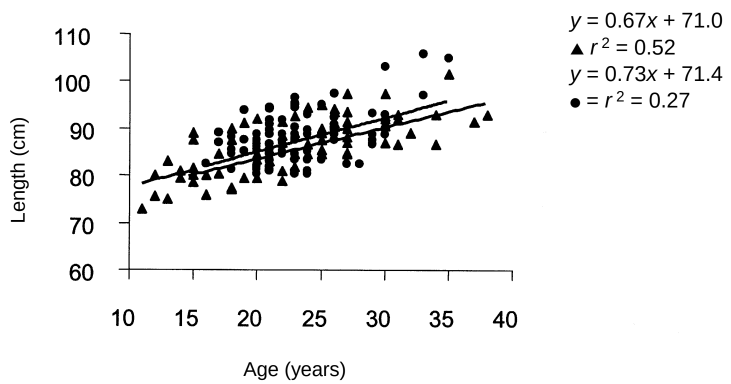

Figure 2

Growth of spiny dogfish in 1987 and 1997. ▲ = 1997 sample (n=79); ● = 1987 sample (n=92).

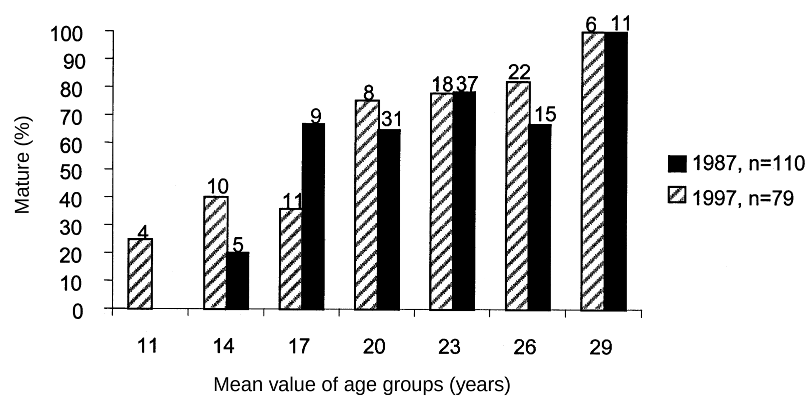

Figure 3

Percentage of mature fish in the different age groups 10–12, 13–15, 16–18,19–21, 22–24, 25–27 and 28–30 years in 1987 and 1997.

1997 sample also had a larger proportion of mature fish less than 15 years of age.

No individual was mature under 76 cm, but all individuals over 88 cm were mature, indicating that maturity occurs between 76 and 88 cm. The length at 50% maturity was 81 cm in both 1987 and 1997. There may be a difference in the growth rate between the two years; fish from 1997 reached maturity earlier than fish from 1987. However, because of the small sample size and difficulty with age determination, caution should be used to interpret this result.

Fecundity

In 1987 the number of ovarian eggs with a diameter over 2 cm (indicating mature fish) varied between 5 and 14 (mean=8.2, SD=2.2). In 1997 the range was 3–17 eggs (mean=8.9, SD=3). The relationship between egg number and adult length in the 1987 and 1997 samples was not significantly different. On average, the egg production increased by one egg per 4-cm adult length.

The number of free-living embryos in 1987 varied from 2 to 14 per female (mean=6.6, SD=2.7). In 1997, free-living embryos numbered between 3 and 15 (mean=7.5, SD=2.6). The increment of free-living embryos per adult length (Fig. 4) in the 1987 and 1997 sample was not significantly different. However, the level of the regression line was significantly higher in 1987 (P=0.04). On average, the females in 1987 carried 1.2 more free-living embryos. It should be emphasized that owing to the large variability, length could only explain 45% to 56% of the difference in the number of free-living embryos.

Reproduction cycle

Eggs on which the blastoderm was visible, were recognized as recently fertilized. This was part of the candle stage (from the newly fertilized eggs up to embryos 10 cm long) that lasted from October to November the following year. Fertilization occurred from the beginning of October to the beginning of February. Free-living embryos were observed from October to September of the following year, followed by parturation of fully mature embryos from September to December. The duration of the pregnancy for spiny dogfish in the Oslofjord ranged from 18 to 24 months. This period of time is calculated from the time of fertilization to the time of parturation. These estimates of the reproduction phases are summarized in Figure 5.

Embryonic growth

The embryos ranged from 4.4 to 24.9 cm total length. The growth of the combined 1986 and 1996 year classes of dogfish embryos was followed throughout their second year of development. Growth was approximately 1 cm per month for both year classes in the size range from 8 to 24 cm, which corresponds approximately to the embryos in the second year of development. However, growth was not uniform; it could be divided into two growth phases (Fig. 6). The first phase lasted from October to May with a slow growth of 0.6 cm/month. The second phase lasted from May until December and was characterized by a more rapid growth of 1.2 cm/month.

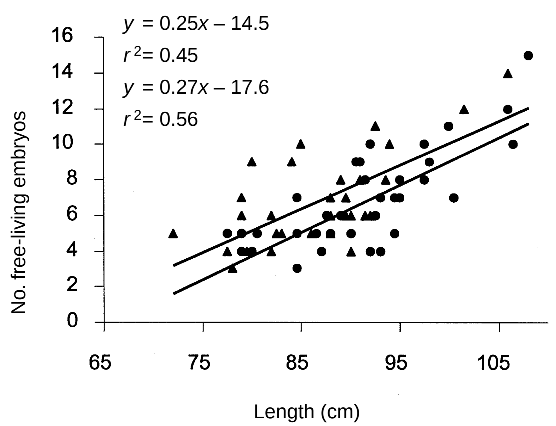

Figure 4

Number of free-living embryos in relationship to the length of the adult fish in 1987 and 1997. ▲ = 1987 sample; ● = 1997 sample.

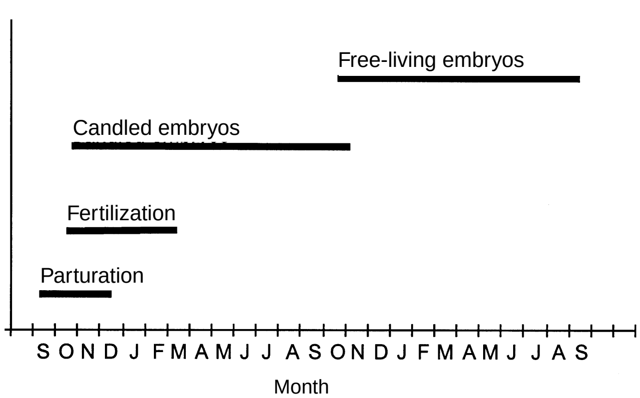

Figure 5

Schematic time representation of the reproductive cycle of the female spiny dogfish by month (n=194).

Discussion

Growth

The lack of an asymptote is probably due to an absence of older, larger fish. This is most likely due to over-harvesting of dogfish in the Oslofjord. According to local fishermen, heavy catches of large individuals (exceeding 110 centimeters) were taken in the late 70s and early 80s.[2]

Age and length at maturity

Age at 50% maturity was found to be 17.6 years in 1987 and 17.0 years in 1997. For spiny dogfish captured between the East Coast of Scotland and Norway, Aasen (1961) estimated age at 50% maturity to be in the range 12 to 14 years. In an area northwest of Scotland, Holden and Meadows (1962) reported age at 50% maturity of 9 years. However, Aasen (1961) and Holden and Meadows (1962) did not take into account worn spines, which combined with the difficulty of identifying all of the annual rings, means that their estimates are most likely biased downwards.

Length at 50% maturity in the Oslofjord should not deviate greatly from sizes observed elsewhere in the northeast Atlantic. Length at 50% maturity in the Oslofjord was found to be 81 cm in both 1987 and 1997. This is in general agreement with other observations in the northeast Atlantic where length at 50% maturity varied from 74 to 83 cm (Hickling, 1930; Holden and Meadows, 1964; Fahy, 1989; Gauld[1]).

Fecundity

There was no significant difference between the number of eggs observed in 1987 and 1997. However, the number of eggs in the ovaries was higher than the number of embryos in the uterus (average: 8.1 eggs and 6.6 free-living embryos in 1987 and 8.9 eggs and 7.5 free-living embryos in 1997). This is probably due to the absorption of eggs in the ovaries following fertilization that was observed by Hanchet (1988), Holden and Meadows (1964), and Nammack et al. (1985).

[2] Johansen, P. A. 1997. Personal commun. Dogfish fisherman from the Oslofjord. Gudeberg Allè 1, 1600 Fredrikstad, Norway.

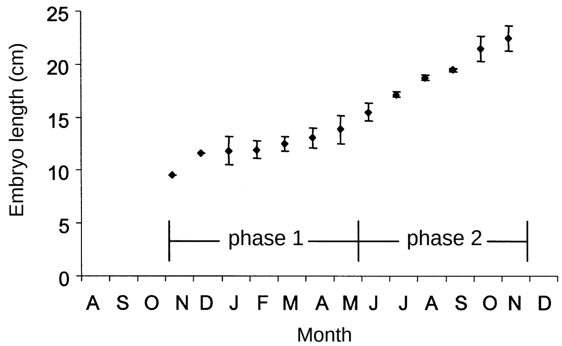

Figure 6
Length of the embryos during their second year of development for the combined 1987 and 1997 sample.

Fecundity was within the bounds found elsewhere in the northeast Atlantic (Aasen, 1961; Gauld[1]). Free-living embryos showed the same increase in number per length in 1987 and 1997, but the level was significantly lower in 1997 (on average one less embryo per unit of length). In addition the fish were shorter and heavier in 1997. However, these results must be taken with some caution because of the large variability in the data.

A small sample size and annual variability in both embryo production and food availability may have contributed to the lower fecundity in 1997. With regard to the sample sizes (31 and 38 fishes), it is emphasized that the covariation between the number of free-living embryos versus length was rather low. Although the differences between 1987 and 1997 were statistically significant, the overlap was so large that caution must be used in interpretation of the data.

Reproduction cycle and embryonic growth

In the Oslofjord, fertilization occurs from October to February and parturation from October to December. Research in other areas has shown that the pregnancy lasts 22–23 months (Ford, 1921; Gauld[1]). Thus, the duration of pregnancy in the Oslofjord (18 to 24 months) seems to have a greater variation than these observations. This variation may have been caused by the sample from the Oslofjord, which included dogfish that were fertilized early in the fertilization period, as well as dogfish that were fertilized towards the end of the fertilization period. This, in turn, indicates the possible minimal and maximal duration of pregnancy.

Behavioral factors may influence pregnancy duration, as well. Some dogfish may inhabit cooler water for longer periods of time than other dogfish, which may increase the duration of their pregnancy.

The differences in the embryo growth rate during their second year of development may be related to the water temperature. Hickling (1930) found that females migrate from deep to shallow water as pregnancy proceeds. This migration pattern exposes the embryos to different temperature levels that may influence embryonic growth, as found in Newfoundland by Templeman (1944). Embryos outside of Newfoundland had an average growth rate of 1.1 cm/month and a 24-month pregnancy period (Templeman, 1944). Outside of Woods Hole, Hisaw and Albert (1947) found an average growth rate of 1.3 cm/month and a pregnancy period of 20–22 months. Nammack et al. (1985) stated that the lower sea temperature outside of Newfoundland could be a possible reason for this difference.

In phase 1, growth is slow and corresponds to a period of low water temperature (winter and spring). As females begin to migrate towards shallower water, they encounter warmer water (summer and fall). The increased growth rate in phase 2 is therefore most likely related to an increase in water temperature.

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Literature cited

Aasen, O.
1961. Pigghå-undersøkelsene. Fisken og havet 1:1–9.
Compagno, L. J. V.
1984. FAO species catalogue. Vol. 4: Sharks of the world: an annoted and illustrated catalogue of shark species known to date. Part 1. Hexiformes to Lamniformes. FAO Fish. Synop. 125:1–249.
Fahy, E.
1989. The spurdog *(Squalus acanthias)* fishery in South West Ireland. Ir. Fish. Invest. ser. B. no. 32, 22 p.
Ford, E.
1921. A contribution to our knowledge of the life-histories of the dogfishes landed at Plymouth. J. Mar. Biol. Assoc. U.K. 12:468–505.
Gilbert, P. W.
1981. Patterns of shark reproduction. Oceanus 24:30–39.
Gordon, D. G.
1986. The spiny dogfish. Oceans 19:56–59.
Hanchet, S.
1988. Reproductive biology of *Squalus acanthias* from the east coast, South Island, New Zealand. N.Z.. J. Mar. Freshwater Res. 22:537–549.
Hickling, C. F.
1930. A contribution towards the life history of the spurdog. J. Mar. Biol. Assoc. U.K. 16:529–576.
Hisaw, F. L., and A. Albert.
1947. Observations on the reproduction of spiny dogfish, *Squalus acanthias.* Biol. Bull. 92:187–199.
Holden, M. J., and P. S. Meadows.
1962. The structure of the spine of the spur dogfish (*Squalus acanthias*) and its use for age determination. J. Mar. Biol. Assoc. U.K. 42:179–197.

1964. The fecundity of the spurdog (*Squalus acanthias*). J. Cons. Perm. Int. Explor. Mer 28:418–424.

Jones, B. C., and G. H. Geen.
1977. Reproduction and embryonic development of spiny dogfish (*Squalus acanthias*) in the Strait of Georgia, British Colombia. J. Fish. Res. Board Can. 34:1286–1292.

Ketchen, K. S.
1972. Size at maturity, fecundity, and embryonic growth of the spiny dogfish (*Squalu sacanthias*) in British Colombia Waters. J. Fish. Res. Board Can. 29:1717–1723.
1975. Age and growth of dogfish, *Squalus acanthias*, in British Colombia Waters. J. Fish. Res. Board Can. 32: 43–59.
1986. The spiny dogfish (*Squalus acanthias*) in the Northeast Pacific and a history of its utilization. Can. Spec. Publ. Fish. Aquat. Sci. 88, 78 p.

Nammack, M. F., J. A. Musick, and J. A. Colvocoresses.
1985. Life history of spiny dogfish off the Northeastern United States. Trans. Am. Fish. Soc. 114:367–376.

Official Statistics of Norway.
1996. Fishery statistics 1961–1996. Graphic Communication Systems, Inc. (GCS) A/S, Oslo, Norway, 116 p.

Saunders, M. W., and G. A. McFarlane.
1993. Age and length at maturity of the female spiny dogfish, *Squalus acanthias*, in the Strait of Georgia, British Colombia, Canada. Environ. Biol. Fish. 38:49–57.

Templeman, W.
1944. The life-history of the spiny dogfish (*Squalus acanthias*) and the vitamin A values of dogfish liver oil. Nfld. Gov., Dep. Nat. Resour., Fish. Res. Bull. 15:1–100.