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Life History of the Piked Dogfish (*Squalus acanthias* L.) in Swedish Waters
(Elasmobranch Fisheries – Poster)

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Abstract

A study of existing literature regarding the piked dogfish (*Squalus acanthias*) behaviour, sexual maturation and age analyses with comparison between the Atlantic Ocean and the Pacific Ocean has been done. Females of the piked dogfish from the Skagerrak were investigated on two occasions during the autumn of 1997. 50% of the females were sexually mature by the age of 12-13 years and 77 cm. The average number of large eggs (>2 cm) were 8.1 and the average number of embryos were 5.8.

Introduction

Aim

The aim with this study was from the beginning to make a population estimation of the piked dogfish, *Squalus acanthias*, in Swedish waters. I wanted to evaluate whether its future could be endangered by the growing demand of shark based products that are the current state for so many other shark species in the rest of the world. To do such an investigation one needs information about, among other things, the age at sexual maturity for both males and females. Literature studies on the subject showed that the piked dogfish is a difficult species to study since it splits into shoals by size and sex. Therefore, the study had to be adjusted to the catch and came instead to be more about the female piked dogfish's life cycle and behaviour in general with age analyses as the main subject.

Structure of the species

The piked dogfish, *Squalus acanthias*, is a common shark in the Atlantic, the Pacific Ocean and in the Black Sea (Jones and Geen, 1976; Polat and Gümüs, 1995). Jones and Geen made 1976 a study regarding whether the piked dogfish in the Pacific Ocean should be classified as a species of their own, *Squalus suckleyi*, as has sometimes been done in other studies, or if it in fact was the same species in both the Atlantic and the Pacific Ocean. After electrophoretic analyses of muscle tissue and blood, comparing morphometric ratios and the number of vertebra on sharks from North Americas east- and west coasts their conclusion was that the differences between the populations were not big enough to classify the population of the Pacific Ocean as a subspecies of the piked dogfish from the Atlantic Ocean. On the other hand many researchers write about the possibility of physiological differences or difference in the metabolic rate that can exist between the sharks in the different oceans. Ketchen (1975) wrote that it seems as if the piked dogfish in the Atlantic Ocean have a more rapid initial growth, become sexual mature earlier and do not attain the same size as its relatives in the Pacific Ocean. Most probably they do not reach the same age either. Something that does not seem to differ between the piked dogfish in the Atlantic and the Pacific Ocean is that it takes between 20 and 23 months for the embryos to develop after fertilization (Holden and Meadows, 1964; Jones and Geen, 1977b). On the other hand Kirnosova (1989) maintains that the piked dogfish in the Black Sea only needs 12 months for the same process.

Migration

That the piked dogfish is a migrating species can both be confirmed by fishermen and through tagging studies. Along the Swedish west coast it is only possible to fish for piked dogfish between August and December since they after that disappears from the area where it is possible to fish them. Also during the autumn the catch can be very variable from day to day since the fish constantly moves (Fourong, pers. com., 1997). There have been discussions whether the piked dogfish in the east Atlantic belongs to one or several populations. Tagging experiments show that it most probably is only one population that migrates along the coasts seasonally (Aasen, 1964; Hjertnes, 1980; Gauld and MacDonald, 1982). In the beginning of the year they stay around the northern part of Scotland from where they move either south to the coast of Ireland or into the North Sea and the Skagerrak in late summer (Hjertnes, 1980; Gauld and MacDonald, 1982). Tag recoveries from the Swedish coast are uncommon in the investigations. If this is because the fishing effort for piked dogfish was not very big at the time of the investigation or if the population here is small and therefore the probability of tag recovery low can only be speculated over here. See "Future studies" later on in this paper.

That there exists only one population in the West Atlantic has been demonstrated by tagging experiments (Templeman, 1976). This population also migrates seasonally. Here the sharks migrate north in the summer to feed outside Canada's coast and when autumn comes they migrate back to the northern East Coast of North America to give birth (Templeman, 1976). Transatlantic migration from east to west has been shown through tagging experiments by Holden (1967) and from west to east by Templeman (1976). It does not seem to be very unusual, but not that common either.

Until they reach sexual maturity, the piked dogfish roam around divided into big shoals depending on size only. The youngest sharks swim near the surface. This has been proven both by food analyses (Jones and Geen, 1977c) and through fishing (Fourong, pers. com. 1997). The older the sharks become the deeper they stay (Wood *et al.*, 1979). After sexual maturity the females and males divide into separate shoals, still in different length classes. The females tend to stay in the middle water and move to shallow water at the time of delivery. In this period they do not feed. The males stay closer to the bottom and farther away from the coast (Hjertnes, 1980; Nammack *et al.*, 1985). The reason for this behaviour is thought to be a reduction in cannibalism. Since the smaller sharks swim close to the surface they are not caught in traditional shark nets that are standing 10 meters over the sea floor. They are instead caught in nets fishing for mackerel in late summer (Fourong, pers. com. 1997). Generally, the bigger females are caught in the shark nets and the males in the trawls fishing for shrimp (Fahy, 1988).

Sexual development

An immature female has small ovaries, non-differentiated eggs and threadlike uteri. A sexual mature female has well-developed eggs in the ovaries and an enlarged, highly vascularized uteri with candles or embryos present (da Silva and Ross, 1993). Earlier studies have shown that the females become sexually mature when they are between 11 and 12 years old in the Atlantic Ocean (Holden and Meadows, 1962; Nammack *et al.*, 1985) and at an age of between 29 (Jones and Geen, 1977b) and 35 years in the Pacific Ocean (Saunders and McFarlane, 1993). It takes two years for the eggs to mature and around 23 months for the embryos to develop. Mature eggs measure 4-4.5 cm in diameter and spawning takes place between December and February. The first 4-6 months the fertilized eggs in each uteri are enclosed in an amber coloured, gelatinous capsule (the so-called candle. See photo no. 1). This capsule then ruptures and the embryos lie after this free in the females' uteri with a big yolk for 16-17 months before they get born in November-December (Photo no. 2 and 3). The pups are then in average 26-27 cm long. New eggs develop during the females' pregnancy and one month after she has given birth she is ready to spawn again (Gauld, 1979; Ketchen, 1972; Jones and Geen, 1977b).



1. Canded eggs

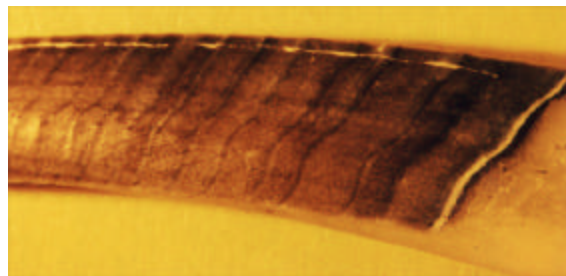
2. One year old embryo, ca 7 cm

3. Two year old embryo, ca 22 cm

The males are considered to be immature if they have undeveloped claspers, small white threadlike gonads and straight spermiducts. Sexual maturity occurs at the age of 5-6 years in the Atlantic Ocean (Holden and Meadows, 1962; Nammack *et al.*, 1985) and at the age of 16-19 years in the Pacific Ocean (Ketchen, 1975; Jones and Geen, 1977b). When they are sexually mature their claspers are big and rigid, the gonads are round and red and the spermiducts are tightly rolled (da Silva and Ross, 1993). Also for the males it takes two years for the sperm to develop, but it seems as if they are able to mate every year since two different stages of the spermatogenesis separated through degenerated tissue always is present after sexual maturity (Jones and Geen, 1977b).

Age determination

Age analyses of elasmobranchs are generally difficult since their placoid scales and otholits are useless for this purpose. Calcified yearly rings in the vertebrae of rays, skates and sharks (Holden and Vince, 1973; Stevens, 1975), x-ray spectrometry (Jones and Geen, 1977a) and length-frequency analysis (Holden, 1972) are some of the methods used in the efforts to age different elasmobranchs. All methods mentioned above are complicated and time-consuming and some of them even useless. The piked dogfish belongs to one of the two shark families that have a spine in front of each dorsal fin. The spine in front of the first dorsal fin is shorter than the one in front of the second and therefore is it more difficult to read (Ketchen, 1975). The spine is like an enlarged placoid scale; that is, it is built up just like a tooth with pulp, dentine and enamel. It differs from ordinary teeth since it deposits pigment between the enamel and the dentine and it never stops growing. The spine is triangular in cross section and hollow. The growth of the spine is continuous over the year, but during the winter it grows slower. It seems like it is only the mantle that increases with the same speed over the year and therefore distinct rings are formed during periods of bad growth in the rest of the spine (Beamish and McFarlane, 1985). These rings often look like ridges on the spines and it is these dark ridges that are counted (see photo no. 4)



4. Distinct rings on a spine base.

That it really is yearly growth behind these rings has earlier been attempted to be proven by indirect methods like length-frequency analyses after von Bertalanffy (Holden and Meadows, 1962; Ketchen, 1975), the basal bands monthly change in colour (Holden and Meadows, 1962), mercury accumulation, differences in length at known stages during the pregnancy and tagging experiments (Ketchen, 1975). After experiments with piked dogfish tagged with Petersen-discs where they also had injected/bathed the sharks in oxytetracycline (= OTC) and recovered the

sharks more than two years later they could state that it really is annual rings that one can count on the spines (Tucker, 1985; Beamish and McFarlane, 1985; McFarlane and Beamish, 1987). The broader light-coloured bands are formed during the summer, and the darker, that one counts, are formed during the winter (Tucker, 1985).

Material and Methods

The field investigation

The piked dogfish were caught on two occasions - the 24 of September and the 29 of October 1997 - north of Väderöarna in the north-western archipelago of Sweden. The fisherman Johan Fourong, that seasonally prosecutes a directed fishery after piked dogfish, caught the sharks on a depth ranging from 30 to 70 m in 10 m high shark nets (10 cm square mesh). The nets were examined and emptied after 24 hours in the water.

On the first occasion 49 females and 7 males were examined and on the second occasion 63 females. On both occasions the spine in front of the second dorsal fin was recovered for age analyses, 102 spines in total. Apart from the spines, the sharks' length, weight, sexual status and stomach content were checked. In the females the numbers of larger eggs, and when occurring also embryos, were counted and size estimated. The male's right claspers were measured from the tip until the edge of the ventral fins. The embryos and the adult sharks' lengths were measured in mm by moving the upper lobe of the tail down so that the snout and the tail were in a straight line (= maximal length) and the weight was rounded off to the nearest hectogram.

The spines were dried and boiled to get rid of meat and skin (Polat and Gümüs, 1995). After drying the spines were kept in small, sealed plastic bags.

Through a Norwegian shrimp research expedition in the Skagerrak, 27-28 October 1997, 10 males and 1 female under 600 mm length came to my disposal. The sharks were caught in trawl and were investigated in the same way as described earlier.

The age analyses

The spines were illuminated from above under 6 times magnification in a stereo microscope. All spines were read two times by the author, with two months between the occasions. The spine diameter of the base and the tip where it has just begun to get worn, from here on called the NWP (No Wear Point), were measured with 0.01 mm accuracy with vernier callipers (Ketchen 1975). Photo no. 5 shows the difference between a worn and a non worn spine.



5. The difference between a non-worn (above) and a worn spine.

A spine is considered to be worn when the diameter at the NWP is more than 2.05 mm (= the calculated average diameter of the spine base one year after birth). The estimated age in spines with NWP <2.05 mm (Y) were then plotted against the diameter of the spine base (X). A regression curve is then calculated and by putting the value of the NWP from worn spines in the curve the number of rings that has been worn off was estimated. This value plus the number of counted rings until the NWP are taken as the corrected age from birth. The spine is on average 1.55 mm at the base when they are born and has two light-coloured bands that had been developed during the time as an embryo, but these are not counted in this study (Ketchen, 1975; Nammack *et al.*, 1985).

Sexual maturity

Females without embryos were considered mature when the eggs were 2 cm or bigger. The males were classified as sexual mature when the spermiducts were tightly rolled and the claspers longer than the ventral fin.

Growth

Growth was calculated according to von Bertalanffy's formula:

$$l_t = L_{\infty}(1 - e^{-K(t-t_0)})$$

where l_t = length at the age t (years)
 L_{∞} = asymptotic length
 K = growth coefficient
 t_0 = age when the fish theoretical length is equal to zero

Results

Age

41 spines were considered to be unworn, that is - the diameter at NWP were less than 2.05 mm. The estimated age were plotted against the diameter of the base in a diagram and since there were so few values they were also compared with Ketchen, 1975; Nammack *et al.*, 1985 (see Fig. 1)

The equation of the curve is:

$$\text{Age} = 0.5735 * \text{Diameter}^{6.7874}$$

After this the values of NWP for the worn spines were put into the equation and the number of rings that had been worn off could be calculated and the age corrected (see Fig. 2)

A 93 centimeter long female had the greatest number of rings. She had 23 rings and correction showed that she was 26 years old. The oldest female was 28 years old and 101 cm long.

Growth

The diameter of the spines' bases showed a correlation to the length of the shark (Fig. 3).

The growth calculated according to von Bertalanffy agrees well to Nammack *et al.*'s results from 1985 (Fig. 4).

The largest shark in the study was a 107 cm female with an age of 23 years.

Sexual maturity

Of the 113 females that were investigated, 14 were not sexually mature (= empty uteri and egg less than 2 cm in diameter). At the age of 12-13 years and a length of 77 cm 50% of the females were sexually mature (Fig. 6 and 7). The largest immature female was 83 cm long and 11 years old and the smallest mature female was 73 cm long and 17 years old.

The largest immature male was 54 cm.

Fecundity

The number of big eggs varied from 4 to 13. The average number of big eggs per female was 8.08 (Table 1). The eggs were either 1.5-2 cm or 4-4.5 cm, which means one or two years old. The number of embryos varied between 1 and 13 per female (Table 2). When there are only one or two embryos in a female it can mean that some foetuses have been aborted due to the fishing. Of the 77 females with embryos in uterus, 39 were due to deliver during this season. The one year old foetuses were around 7 cm long during the first investigation in late September and they had external gills. One month later they were between 9 and 11 cm in length and with internal gills. Their yolk sacks were at both occasions ca 6 cm in diameter. The embryos that would be born this season (most likely between November to January) were between 18 and 25 cm in length. The size at the time for delivery is partly depending on the size of the mother. During the first occasion of investigation these embryos had external yolk sacks that were

less than 1 cm in diameter. In October, the yolk had in most cases been fully absorbed and only a non healed slit could be seen on the abdomen.

Two females contained candles in October. One of these had 10 eggs that were 2 cm big and one embryo that was 11 cm long. Consequently, it seems like the fertilized eggs (in the candle) had not wandered into the uterus, but they had not been resorbed or pushed out either.

Diet

Since the females do not feed at the time for delivery, most of the animals had empty stomachs. In some it was possible to distinguish remains of octopus, crayfish and white fish.

Discussion

To be able to give a fairly true picture of a population a representative sample is needed. This is unusually difficult with the piked dogfish since they divide into different shoals depending on size and sex. During the two occasions when the fish was caught the fisherman got almost only females between 70 and 100 cm in length and therefore the sample was not representative for the whole population.

Age analyses

Since the spine constantly grows the earliest rings are worn off and if one does not compensate for this the age is underestimated and the growth rate overestimated (Holden and Meadows, 1962; Ketchen, 1975). Ketchen modified and simplified Holden and Meadows method to estimate the number of rings that has been worn off and therefore Ketchen's method was used in this study. Holden and Meadows 1962 described in detail different types of rings and characterized many rings as false. This could have led to that they underestimated the age of the piked dogfish. After reading the spines, I am willing to agree with Ketchen, 1975 that the rings show so much of individual variation regarding colour, width and the appearance in general that to decide special criteria for rings validity is impossible. Consequently, all rings that were fairly distinct have been counted as a true annual ring. This procedure may have led to an overestimation of the age, but since the growth in the piked dogfish is slow and non continuous, which Holden and Meadows didn't assume (Ketchen, 1975) it seems logical to follow Ketchen's procedure. (Ketchen gives in his paper from 1975 several examples of tagging investigations where the sharks by the time of recapture show a zero growth or even a decrease in length.)

Only the author has read the spines. The interpretation error has therefore not been estimated. In earlier studies one to three people have read the spines and in many cases they have also read the spines several times to get a more certain picture. One person reading the spines (Soldat, 1982; Beamish and McFarlane, 1985; Tucker, 1985), two persons (Holden and Meadows, 1962; Ketchen, 1975; Nammack *et al.*, 1985 (2 times); Fahy, 1988; Saunders and McFarlane, 1993; Polat and Gümüs, 1995), three persons (McFarlane and Beamish, 1987). They have compared the results between the different readings to find agreement and have rejected spines where the age has been disagreeing by more than two years. In this study it has not been possible to compare the two readings since they were done in different ways. The first time all rings were counted, also those that could be seen where the spine was worn. The second time all rings until NWP were counted and after measuring the diameter at NWP, the number of rings worn off was estimated.

Growth

It has been mentioned several times that the growth of the piked dogfish is slow. Little is known about the growth of dogfish in the first years after birth, since they generally are absent from commercial fishing. But it seems like the growth until sexual maturity is faster. After sexual maturity growth is only about one cm a year, and there are examples of zero growth or even shrinkage (Ketchen, 1975).

Sexual maturity

Most authors consider it difficult to decide when a female piked dogfish is sexual mature, if there are no eggs present. Since it takes two years for the eggs to develop to mature size (ca 4.5 cm), they are around 1.5-2 cm big after one year. The question is then whether one should consider the female sexually mature when she is ready to spawn for the first time or one year earlier when the eggs are developing. In earlier studies the authors have considered the females sexually mature by different sizes of the eggs: 1.5 cm (Nammack *et al.*, 1985; da Silva and Ross, 1993), 2 cm (Saunders and McFarlane, 1993), 2.5 cm (Ketchen, 1972), 3-4 cm (Fahy -88; Gauld, 1979), "large

eggs" - 4 cm mature (Jones and Geen, 1977b), - 4.5 cm (Kirnosova, 1989), "large eggs" (Holden and Meadows, 1962, 1964). I have chosen to consider females with eggs larger than 2 cm as sexually mature. Such females would have spawned next autumn and have most probably already begun to grow slower since they are developing the big, nutritious eggs. Of the 23 females that only contained large eggs, 4 had eggs between 2 and 3 cm in size.

The estimated age of 50% sexual maturity is similar to the results from other studies from the Atlantic (Table 3).

Fecundity

Fecundity can be calculated in three different ways, viz. by counting 1) ovarian eggs (Table 4) 2) fertilized eggs - the so called candles 3) the embryos in uterus (Table 5). The ovarian eggs can be bad or sterile and therefore some eggs are often resorbed or expelled – comparing between the average number of eggs and embryos give that the number of eggs is always bigger (compare Table 4 and 5). It is important that the parent is of average size for the population when population estimations are made from the number of embryos since the number of embryos partly depends on the size of the female (Ketchen, 1972). Embryos, especially those who are nearly fully developed, are also aborted rather easily from the female during capture. The most reliable way to estimate fecundity, according to Fahy, 1989, would therefore be to count the fertilized eggs (in the candles). This stadium occurs mainly during springtime (during the investigations in the autumn only two females contained candles) and that is the period when the piked dogfish disappears from the Swedish coast.

Diet

The results from investigation of the sharks' stomach contents agree well with earlier investigations on the subject. In the north of the Pacific Ocean, outside the coast of Canada, the piked dogfish has for a long time been accused by the local fishermen to eat commercially valuable fish, like salmon, and they were therefore for a long time considered to be a noxious animal. It is partly therefore Canada has done so many studies on the piked dogfish. Jones and Geen (1977c) and Tanasichuk *et al.* (1991) came to the conclusion that piked dogfish mainly eat herring, Pacific hake, Crustaceans and Molluscs in the Pacific Ocean. The importance of fish in the diet increases with the age of the shark.

Conservation

Many of the studies mentioned, has been performed to investigate if the piked dogfish is a threatened species or if it is possible to exploit it even more. Holden and Meadows (1964) stated in their study that the reproduction potential of the piked dogfish was below the level at which they would be able to replace the population under prevailing fishing pressure. Also Aasen (1964) warned that the current fishing pressure was too high for the population of piked dogfish, and this led to the introduction of a minimum size of 70 cm for piked dogfish in Norway. Gauld (1979) thought that Holden and Meadows (1964) were wrong and stated that the piked dogfish can compensate for the fishing by an increase in fecundity, but of course only up to a certain level. Hjertnes (1980) demands intensified research and believes in a regulation of the fishing for the piked dogfish through international catch quotas and a protection of the older (= larger) females. Nammack *et al.* (1985) are warning for an over exploitation of females when minimum sizes are introduced and therefore they want catch quotas by sex but also a change in the demand from the market, that is a bigger demand for smaller sharks.

In the Pacific Ocean there is not the same problem as in the Atlantic Ocean since the piked dogfish is relatively unfished there since the Second World War. They have more considered the piked dogfish as a noxious animal that eats salmon and herring and destroys fishing-gears. Ketchen (1975) had the opinion that the life-history and biology of the piked dogfish should be carefully investigated so that an eventual control program or even better, an exploitation of the resource could begin. Jones and Geen (1977b) did not want to restrict the mesh size but to introduce an annual fishing quota and Wood *et al.* (1979) wrote that nothing speaks for a minimum size. I think that before any further studies are done, to be on the safe side, one should harvest only the males. It is very easy to distinguish the males among the females and since the females appear along the Swedish coast to give birth, they should be spared.

Future studies

It is often said that the piked dogfish is a species that migrates very much and over great distances. But no tagging experiments have been performed along the Swedish west coast and only a few individuals that have been tagged in the North Sea and outside the Norwegian coast have been recaptured here (Aasen, 1964; Hjertnes, 1980; Gauld,

1982; Gauld and MacDonald, 1982; Tucker, 1985). Where do the "Swedish" piked dogfish go when they disappear from the Swedish coast in December? Do they swim to other areas and get caught there or do they gather themselves in non fishing depths, in for example Kosterrännan, as the Swedish fishermen believe (Fourong, pers. com. 1997). With a new kind of tags, so called popup-tags, that combines data logging and satellite transmission one can get an answer to the question. The tag collects data as depth, light, temperature and time and after a predestinated period on the back of the shark it lets go and rise to the surface where the information is taken care of by a satellite. Since it is not necessary to recapture the shark, which is a necessity with an ordinary data log tag, the chance of getting the information back is bigger. A traditional satellite tag does not work on a piked dogfish since it has no behaviour of swimming close to the surface.

Since the piked dogfish is growing very slowly, produces only a few pups every second year and the demand for shark based products have risen in the world in later years, it lies in our interest to investigate their ecology more, so that they are not threatened by over fishing in a close future. The fishing in Sweden is small today - in 1997 214 tons were landed and approximately half of it came from the specific shark fishing. But if the piked dogfish leave the Swedish coast to migrate out in the North Sea, they run the risk of being caught also there. Can the species stand the fishing pressure?

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Table 1. Number of females with large eggs (>2 cm) in the ovaries distributed after the length of the female and the number of eggs.

Total length females, cm	Number of females with 4 to 13 large eggs in the ovaries											Average number eggs/female (SD)
	4	5	6	7	8	9	10	11	12	13		
70-74	1											7.00 (0)
75-79	1	2	4	3	2							6.25 (1.22)
80-84	3	2	7	1	3							6.94 (1.34)
85-89	1	5	10	4	1	3	2					7.62 (1.63)
90-94	1	3	3	5	2	3	5	1				8.65 (2.01)
95-99	1		3	2	1							10.00 (1.91)
100-104	1			4	1	1						11.00 (1.53)
105-109				1								12.00 (0)
Total	1	7	15	24	13	6	9	13	4	1		8.08 (2.15)

Table 5. Comparison between different studies of the number of embryos per female divided into different length classes.

Study	Area	Length female, cm	70-79	80-89	90-99	100-109	Average
The Atlantic Ocean							
Holden and Meadows 1964	The North Sea				3.4	4.8	6.6 8.7 5.8
Gauld 1979	The North Sea			1.9	5.4	8.8	12.2 7.1
Nammack et al 1985	The Northwest Atlantic Ocean					3.9	6.2 8.6 6.6
Fahy 1989	The North Sea				4.6	6.0	7.3 6.0
This study 1997	The Skagerrak			4.9	4.9	6.8	8.5 5.8
The Pacific Ocean							
Ketchen 1972	The Northeastern Pacific Ocean					3.8	5.8 7.8 6.6*
The Black Sea							
Kirnosova 1989	The Black Sea				7.4	10.1	14*

* In the Pacific Ocean and in the Black Sea the piked dogfish become sexually mature at a bigger size than in the Atlantic and the females can become up to 130 and 145 cm respectively in length. This lead to that the average number of embryos is higher than the table shows.

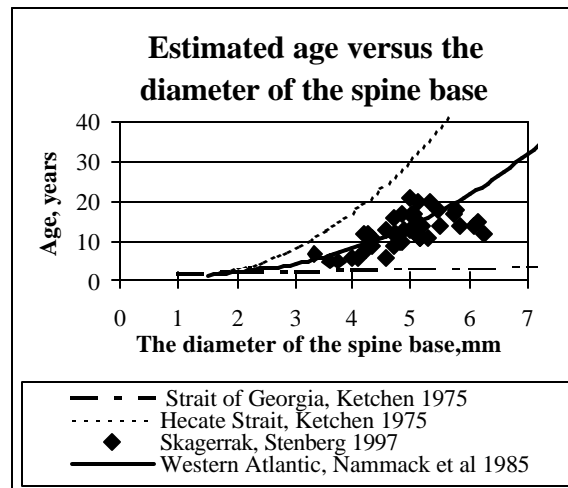


Fig. 1. Estimated age *versus* spine base diameter. Comparison between The Pacific Ocean (Ketchen, 1975), The Northwest Atlantic Ocean (Nammack *et al.*, 1985) and The Skagerrak (This study).

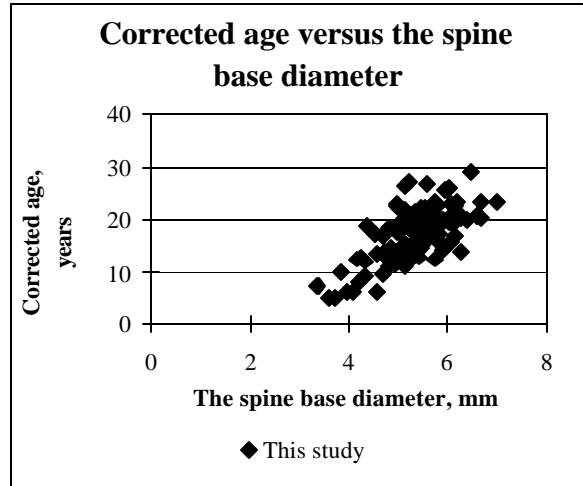


Fig. 2: The corrected age *versus* the diameter of the spine base

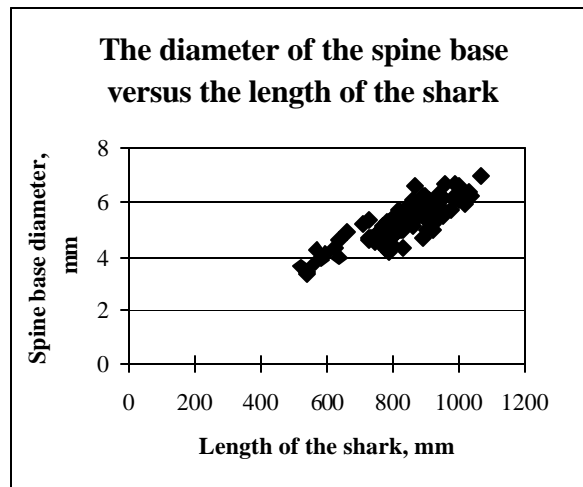


Fig. 3: Comparison between the diameter of the spine base and the length of the shark.

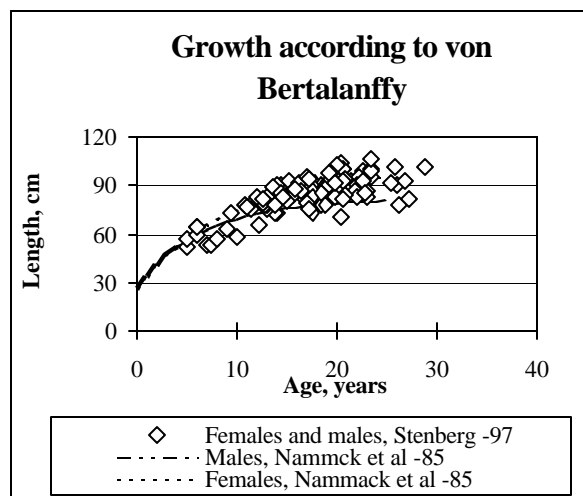


Fig. 4. Comparison of growth after von Bertalanffy between the Northwest Atlantic Ocean (Nammack *et al.*, 1985) and The Skagerrak (This study).

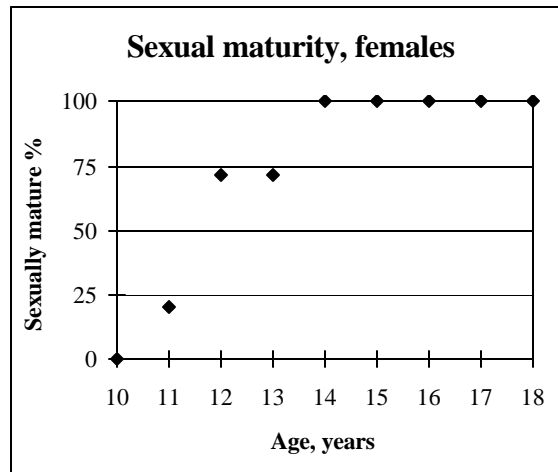


Fig. 5. Sexual maturity (%) *versus* age.

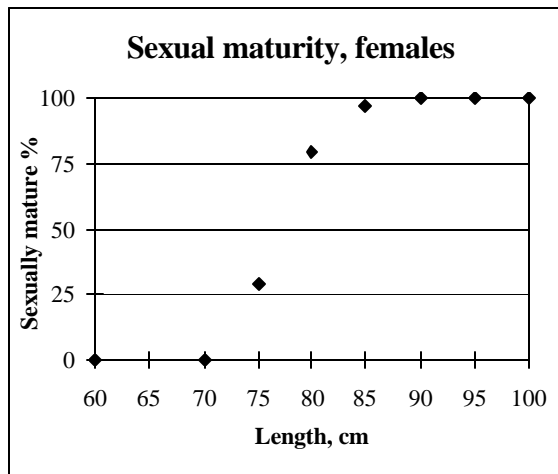


Fig. 6. Sexual maturity (%) *versus* the length.