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Age at sexual maturity and reproductive performance of the female hooded seal (*Cystophora cristata* Erxleben) in South Greenland

by

E. W. Born

Zoological Museum
University of Copenhagen
Universitetsparken 15
DK-2100 Copenhagen Ø, Denmark.

Abstract:

Reproductive organs of 105 female hooded seals from South and South East Greenland were collected in 1970-71 in the period from 20 of April to 19 of July. Ages from tooth cement analysis were available from 95 of the specimens.

In this paper some supplementary details on the gross anatomy of the reproductive organs of the female hooded seal are presented.

From the distribution of age at the first ovulation of the combined South and South East Greenland sample (N: 95) it was found that sexual maturity is attained from 2 years of life (19.6%) to 9 years of life (4.6%) with 3.2 years as the median age of sexual maturity. The estimate of the reproductive rate, obtained from indirect methods of determining the reproductive success, was found to be 0.936 young per mature female per year for 3 to 22 years old females. One instance of implantation of the blastocyst was found on 29 July.

Introduction: Information on the reproductive biology and sexual maturity of the female hooded seal in the Greenland Sea in 1956-59 was presented by Popov (1960). Øritsland (1964) gave further information on the reproductive biology and sexual maturity of the female hooded seal at the moulting area in Denmark Strait and on the breeding grounds at Jan Mayen in 1956-60. Also data of the sexual maturity and reproductive performance of the female hooded seal are available from the breeding grounds at Newfoundland-Labrador in 1967-72 (Øritsland 1975).

This report presents supplementary information on the breeding cycle, sexual maturity and

sexual performance of the female hooded seal from South and South East Greenland 197o-71. The material analysed was collected during the spring migration of the hooded seals from Newfoundland to the moulting areas in Denmark Strait (Kapel 1972, 1974 and 1975).

Material: As a part of the Danish seal research program in Greenland a total of 1o5 female reproductive tracts from hooded seals were collected in South and South East Greenland. In South Greenland (6o° to 61° N) 99 reproductive organs with lower canines for age determination were collected in the period from 2o of April to 2o of June. Six of these specimens were collected in 197o and the rest in 1971. Furthermore, 6 reproductive organs from Angmagssalik in South East Greenland have been included in the analysis. These specimens were collected from 18 to 29 of July. So the combined material of female reproductive organs from hooded seals in South and South East Greenland represents the period from 2o of April to 29 of July, which is covering most of the period of delayed attachment of the blastocyst to the uterine endometrium, according to Øritsland (1964).

Of 1o5 female reproductive organs 95 are accompanied by ages obtained from analysis of the cementum growth layers, as described by Kapel (1972 and 1975). However, in the following the remaining 1o reproductive organs without known ages have been included in age-independent descriptions of the gross anatomical structures of the reproductive organs.

The age composition of the sample of female reproductive organs is shown in Fig. 1. The underrepresentation of youngs of the year and one and two-years-olds is readily evident. However, the age distribution of the sample is very similar to the age distribution of the catch of female hooded seals in South Greenland, as described by Kapel (1972, 1974 and 1975).

Methods: The reproductive organs were fixed and stored in 4 % formalin. At the laboratory the ovaries were cut by hand in about 2 mm thick sections, by scalpel. The uterine horns were slit

longitudinally and transversally to locate the blastocyst. The volume of the ovaries was measured and also the length of the uterine horns along the anterolateral surface from the ovarial bursa to the termination of the horns in the corpus uteri. Similarly, two diameters of the uterine horns were measured at the midpoint of the horns. All follicles were counted and two diameters of the largest follicle, the corpus luteum and all corpora albicantia were recorded.

Results: A detailed description of the breeding cycle and the gross anatomy of the ovaries of the female hooded seal in the period of delay of attachment of the blastocyst has been given by Øritsland (1964) so only a few supplementary details are added in this report.

Uterine horns and ovaries: Three phases of growth were observed in the uterine horns and the ovaries. There is an age related phase of growth of the uterine horns and the ovaries up to about the fifth year when there is a less pronounced increase in size up to about the 22^{nd} year. Imposed on this pattern of growth there is an increase in size in the reproductive organs in connection with attainment of sexual maturity (i.e. first ovulation). From the attainment of sexual maturity there is a cyclic change in size related to the function of the ovaries and the uterine horns in the annual breeding cycle. An essentially similar pattern of growth was reported by Øritsland (1964) for the female hooded seal and is characteristic for most seals (see for example Hewer 1964 and Smith 1973),

The post partum changes in the uterine horn are recognizable as increased diameter and hyperaemia of the myometrium and the endometrium for about 3-3.5 months post partum. This feature is important in deciding the proper interpretation of the large corpora albicantia as whether they belong to successful pregnancies in the preceding breeding cycle or are regressing corpora lutea of ovulation in the current breeding cycle. The average diameter of the uterine horn with post partum changes is 23.1 mm (SD: 4.78) and the average diameter of the other horn is 2o.8 mm (SD: 4.83). This difference is significant at the 1 % level ($P < o.ol$, $t = 3.126$, df: 162).

Despite a close examination of the lumen of the uterine horns I detected no blastocysts. However, in a 15-year-old animal a swelling (about 9 mm in diameter) of the uterine horn adjacent to the ovary with the new corpus luteum apparently represented the nidation site of an undetected blastocyst. This specimen was killed on the 29 of July which is in the period of the attachment of the blastocyst, according to Øritsland (1964).

Follicles: Because a lack of one and two-years-olds in the material little can be said about the follicular stimulation in association with the approaching sexual maturity. However, in immatures of all ages (2 to 7 years) both ovaries contained about 5o follicles on average (Mean 49.4 follicles per ovary, range: 2 to 119 follicles, SD: 41.4, N: 2o) while 3 immatures (23 %) had no macroscopically visible follicles at all. Among these latter was a one-year-old specimen. The large individual variation in the number of follicles observed in the material from Greenland in both immatures and matures is also reported by Øritsland (1964) and is common to most seals during the same period of the breeding cycle (e.g. Pearson and Enders 1951, Fisher 1954, Craig 1964).

In the period from 2o of April to 29 of July there is a decrease in the average number of follicles in the ovary containing the new corpus luteum from about 25 follicles to about 17 follicles per ovary. This decrease was exclusively due to the fall in the number of follicles smaller than 3 mm in diameter while the average number of larger follicles was constant in the period. As suggested by Øritsland (1964) this development may reflect the growing hormonal activity of the corpus luteum. In the ovary with the regressing corpus luteum of the preceding breeding cycle (now the corpus albicans) the average number of follicles was low (ca. 7 follicles per ovary), reflecting the fact that the regressing corpus luteum retains it follicle depressing effect for at least 3-3.5 months post partum, as already described by Øritsland (1964). There was no trend in the average size of the largest follicle in either of the ovaries in the period from 2o of April to 29 of July.

Twenty-five specimens were found with follicles larger than 1o.o mm in average diameter. Of

these, two were immature with follicles 12.7 and 11.6 mm in diameter, respectively. These animals (2 and 3 years) were approaching sexual maturity but in the remaining specimens, which were all mature, some of the follicles had reached the preovulatory size (here: 13.1 to 15.6 mm) but had apparently been prevented from ovulating by the new corpus luteum. In a 22-year-old (18 July) a partly luteinized follicle (14.6 mm in diameter) was associated with a apparently healthy corpus luteum. A similar situation is described for the ringed seal (Pusa hispida) by Smith (1973).

Only a few aberrant follicles were found. In a 3-year-old newly-mature animal several haemorrhagic follicles were situated in the inactive ovary. In a 3-year-old immature and in a 7-year-old mature several small follicles had an orange gelatinous content. These follicles resembled those described by Craig (1964) and Smith (1973), according to whom such follicles may represent follicles that were depressed in a phase of active growth.

Corpus luteum: Of 84 corpora lutea 12 (14.3 %) showed no macroscopic sign of vascular or connective tissue intrusion. In the rest of the corpora lutea the vascular elements and the connective tissue had developed to a varying degree with no apparent relationship to the time of capture, and none of the corpora lutea showed features of advanced degeneration usually related to regressing corpora lutea of ovulation or pseudopregnancy (cf. for example Pearson and Enders 1951, McLaren 1958 a, 1958 b, and Bigg 1969). Seven animals were found with fluid-filled antrum or ovulation cavities in the corpus luteum. The size of the fluid-filled cavities showed no relationship to the time and for obvious reasons it is impossible to state whether some of these vesicular corpora lutea represented extra-seasonal infertile ovulations as suggested by Øritsland (1964). However, similar fluid-filled corpora lutea have been described from normal pregnancies in several other seals (e.g. Pearson and Enders 1951, Harrison et al. 1952, Craig 1964 and Øritsland 1968). In his study of the female hooded seal in Denmark Strait Øritsland (1964) categorized some fluid-filled corpora lutea as corpora lutea from infertile ovulations. In treating the material from Greenland I have regarded the fluid-filled corpora lutea as representing

normal pregnancies as they were all in apparently healthy reproductive organs. According to Øritsland (pers. comm.) there is a marked difference in appearance between the early stages of corpora lutea graviditates and corpora lutea of ovulation so it is most likely that the fluid-filled corpora lutea in the Greenland sample were all corpora lutea of true pregnancies. The interpretation of these vesicular corpora lutea will affect the estimates of the reproductive success obtained from the presence of the corpus luteum in the period of delayed attachment of the blastocyst. Such corpora lutea made up 9.2 % (7 of 76) of all corpora lutea in the animals of known age from Greenland.

In the period from 2o of April to 29 of July the average diameter of the corpus luteum increased by 33 % from ca. 12 mm to ca. 16 mm. A similar increase in size in this period was observed by Øritsland (1964).

Corpora albicantia : Of 92 sexually mature specimens 82 had a large normal corpus albicans associated with a uterine horn which showed post partum changes. The average diameter of this largest corpus albicans is 9.3 mm (range: 6.o to 13.5 mm, SD: 1.77, N: 82). In late July the corpus albicans has decreased to about 75 % of its size in late April, that is to an average diameter of 7.3 mm. In the corpus albicans brown traces of regressing luteal tissue are still evident among the fibrous tissue. A nearly perfect alternation in the functioning of the ovaries in the annual breeding cycle was found as 98.7 % (76 of 77 animals) had a new corpus luteum in the ovary opposite the ovary with the largest corpus albicans. A less perfect alternation was observed in the position of the largest and the second largest corpus albicans. About 22 % (12 of 54 animals) of the specimens with more than one corpus albicans in the ovaries had the two largest corpora albicantia situated in the same ovary. This partly reflects the varying regression rate of the individual corpora albicantia, already observed in the largest corpus albicans making it more difficult to separate generations of corpora albicantia from size characteristics alone. The second largest corpus albicans is a connective tissue core with a mean diameter of 6.3 mm (range: 3.o to lo.5 mm, SD:

1.43, N: 54). The size frequency distribution of the other corpora albicantia, other than the two largest, is a symmetrical normal distribution (mean diameter: 4.8 mm, range: 3.2 to 7.1 mm, SD: 1.01, N: 66). This reflects the fact that it was impossible to separate different stages of regression in the group of small corpora albicantia from size characteristics or structural features.

The accumulation of corpus luteum and corpora albicantia in the ovaries is shown in Fig. 2. There is an increase in the average number of corpora in the ovaries up to about 7 to 10 years of life, when old corpora albicantia appear to be absorbed in the ovarial stroma. From the second to the seventh year the average accumulation rate is 0.41 corpora lutea and albicantia per individual per year and from the eighth year of life to about the twenty-second year the average accumulation rate is 0.21 corpora per individual per year.

I found no criteria for separating different stages of regressing corpora albicantia as originating from successful pregnancies or infertile ovulations (regressing corpora lutea of ovulation) by structutural appearance. This difficulty can be attributed to the fact that the material was collected in the early period of the breeding cycle when corpora lutea from infertile ovulations had not yet regressed. However, in 7 individuals the corpora albicantia were associated with immature uterine horns that had not carried any pregnancies, indicating that the corpora albicantia were from infertile ovulations. In four first-time ovulating animals (3, 3, 4 and 6 years) this corpus albicans was the only trace of an ovulation. A 6-year-old (25 of May) had a 11.7 mm new-looking corpus albicans with regressing luteal elements in one ovary, apparently being a regressing corpus luteum of ovulation. Three animals had one corpus albicans in each ovary, both being associated with immature uterine horns. One of these animals was an 11-year-old killed on the 20 of April. The similarity of all these corpora albicantia of infertile ovulations to corpora albicantia of assumed normal pregnancies indicates that during this period of the breeding cycle the two categories of corpora albicantia can be confused. Retention for some time of the traces of infertile ovulations may also account for the finding in 21 % (6 of 29 animals) of the young

specimens of the only two corpora albicantia situated in the same ovary.

Age at sexual maturity: An individual having either a corpus luteum or a corpus albicans in the ovaries is regarded as being sexually mature.

In this study the method of determining the age at sexual maturity from the number of corpora lutea and corpora albicantia is similar to the method described by Øritsland in his studies of the sexual maturity of the female hooded seal (Øritsland 1975) and the female harp seal (Pagophilus groenlandicus) (Øritsland 1971).

In the sample of female hooded seals from Greenland, collected during the delayed attachment of the blastocyst, the age at last ovulation is the same as the age obtained from tooth cement analysis. In this study the maturity analysis is based on the presence of the 3 last corpora in the ovaries i.e. the new corpus luteum, the large corpus albicans from the preceding breeding cycle and the second largest corpus albicans, which is assumed to represent a breeding cycle that ended about a year before capture.

The result of the analysis is shown in Table 1 and the accumulated maturity frequencies are depicted in Fig. 3. The individual ages of the first ovulation ranged from 2 to 9 years of life. In the combined sample of female hooded seals from Greenland 5o % of the animals had experienced their first ovulation by the age of 3.2 years and all were sexually mature by the 1oth year of life.

Estimates of the reproductive success from incidence of successful ovulations: Three different methods of estimating the reproductive success of the female hooded seal were applied to the sample from Greenland. These methods depend on the interpretation of indirect evidence of pregnancy i.e. the corpus luteum or the corpora albicantia.

1) If the presence of an apparently normal corpus luteum, including those with a fluid-filled antrum, is regarded as evidence of a pregnancy (a successful ovulation) in the period of delay, then the ratio of animals with a corpus luteum to all mature

animals in the sample will give an estimate of the reproductive success during this period of the breeding cycle. The figures from the female hooded seals from Greenland are presented in Table 2 (row 1).

2) If one estimates the reproductive success from the latest corpus albicans, only a large normal-looking corpus albicans associated with a uterine horn with post partum changes is regarded as representing a pregnancy in the preceding breeding cycle. The ratio of these corpora albicantia to the number of corpora albicantia associated with immature uterine horns or uterine horns with no post partum changes will give an estimate of the pregnancy rate based on the corpora albicantia. The results of this analysis is shown in Table 2 (row 2).

3) The method of determining the ave rage reproductive success of annually breeding seals from numbers of " missing " corpora in an assumed perfectly alternating sequence of corpora albicantia in an individual was applied to the material of hooded seals from South Greenland. The principles of the method were outlined by Øritsland (1971 and 1975). Applying the method to the material from Greenland only the corpora lutea and corpora albicantia from the 3 last breeding cycles were considered. Corpora albicantia which were associated with reproductive tracts with no signs of earlier pregnancies were disregarded in this analysis. The results of the analysis are seen in Table 2 (row 3) and in Table 3.

The average estimate of the reproductive success of the female hooded seal from Greenland in the age-group 2 to 10 years is 0.919 young per mature female per year and in the age-group 11 to 22 years the estimate is 0.964 young per mature female per year. For all age-groups the estimate of the reproductive success is 0.936 young per mature female per year. None of the different estimates obtained from the three methods differed significantly at the 5 % level (Estimates of the reproductive success: 2 - 10 years: χ^2 = 5.04, 90% < P < 95 %, df. 2. Estimates from 11 to 22 years: χ^2 = 2.14, 60% < p < 70 %, df: 2. After Hald 1971).

The estimates of the overall reproductive success of the female hooded seal obtained in the studies by Øritsland (1975) and in this study is o.952 young per mature female per year. The results of the different studies are shown in Table 4. None of the three estimates of the average reproductive success differed significantly at the 5 % level (χ^2 = 5.82, 9o % < P < 95 %, df: 2. After Hald 1971).

Discussion: Øritsland (1975) presented accumulated frequencies of sexually mature female hooded seals from Newfoundland-Labrador (2 samples) and from Denmark Strait (recalculated from Øritsland 1964). There was no difference between the maturity frequencies of the three samples of female hooded seals at the 5 % level (Øritsland 1975). The maturity frequencies in this study of the female hooded seal from Greenland did not differ from any of the accumulated maturity frequencies given by Øritsland (1975). Data from Øritsland (1964) were recalculated according to the methods suggested by Øritsland (1975) (P < o.o5, Kolmogorov-Smirnov two-sample test after Siegel 1956).

The similarity of the estimates of the reproductive success obtained in this study to the estimates presented by Øritsland (1964 and 1975) confirms the statement given by Øritsland (op.cit.) that the reproductive success of the female hooded seal is actually very high. The close fit of the estimates of the average reproductive success from three different areas of the range of the hooded seal in the Northwestern Atlantic to the pregnancy rate of o.95 suggested by Øritsland (1975) indicates that this rate is realistic for management purposes.

As indicated in the section on the corpora albicantia there may be some fallacies in assuming that a break in the normal size sequence of corpora albicantia in an individual necessarily indicates that the animal has missed a pregnancy in one of the breeding seasons. At any rate in the period of delayed attachment of the blastocyst some of the observed differences in the number of corpora albicantia in the two ovaries of an animal may as well be ascribed to the retention of scars from infertile ovulations, or to a less perfect

control of the ovulation mechanism in the younger age-groups. The somewhat higher frequencies of missed pregnancies observed in my study as compared to the frequencies from lactating females (before the new ovulation) given by Øritsland (1975) may well be due to the resorption of corpora from infertile ovulations at term.

However, the similarity of the estimates of the reproductive success obtained by the different methods in my study and the possibility of excluding some corpora albicantia as originating from definite infertile ovulations support the idea that the average reproductive success may well be estimated from the sequence of corpora albicantia, as suggested by Øritsland (1971 and 1975). Furthermore, the similarity of the estimates of the reproductive success obtained from examination of the corpus luteum and the corpora lutea indicates that the incidence of ovulation serve as a reliable indicator of pregnancy in the female hooded seal.

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TABLE 1. The distribution of age at sexual maturity (first ovulation) of female hooded seals in a combined sample from South and Southeast Greenland 1970-71; (20 Apr. - 29 Jul.).

Age in years	No. total	No. mature	Age at first ovulation 1	2	3	4	5	6	7	8	9	10
1	1	0	-									
2	4	1	-	1								
3	12	7	-	6	1							
4	13	11	-	2	9	0						
5	8	7	-	1	2	4	0					
6	5	5	-	-	-	4	1	0				
7	8	7	-	-	-	1	5	1	0			
8	7	7	-	-	2	0	1	4	0	0		
9	6	6	-	-	-	-	1	1	2	1	1	
10	4	4	-	-	-	-	-	1	1	1	1	0
Sum	68	55	0	10	14	9	8	7	3	2	2	0
Sum mature within the last 3 years		46	0	9	12	8	6	5	2	2	2	0
Per cent mature			0	19.6	26.1	17.4	13.0	10.9	4.3	4.3	4.3	0
Accum. percent				19.6	45.7	63.1	76.1	87.0	91.3	95.6	99.9	99.9

Table 2. Age-specific reproductive success (incidence of ovulations) of the female hooded seal from South and South East Greenland 197o-71 estimated from three different methods.

Age-groups: 2 to 1o years of life (ages incl.)

		n	x	Estimate of reproductive success. x/n
1.	Corpus luteum	55	5o	o.9o9
2.	Largest corpus albicans	45	38	o.844
3.	No. of " missing " corpora albicantia	121	115	o.95o
	Total	221	2o3	o.919

Age-groups: 11 to 22 years of life (ages incl.)

1.	Corpus luteum	27	26	o.963
2.	Largest corpus albicans	37	37	1.ooo
3.	No. of " missing " corpora albicantia	73	69	o.945
	Total	137	132	o.964

Overall rates of reproductive success: Age-groups: 2 to 22 years of life (ages incl.)

1.	Corpus luteum	82	76	o.927
2.	Largest corpus albicans	82	75	o.915
3.	No. of " missing " corpora albicantia.	194	184	o.948
	Total	358	335	o.936

n = total no. of breeding cycles

x = total no. of successful breeding cycles (i.e. presumed pregnancies).

Estimates of reproductive success in young per mature female per year.

Table 3. The reproductive performance of mature female hooded seals from South and South East Greenland 197o-71. The rate of presumed pregnancies (i.e. incidence of successful ovulations) through the last three breeding seasons is estimated from corpora albicantia missing in a regular size sequence between the two ovaries from each animal. (Total no. include 'No. missing ').

age-group in years	total no.	no. missing	% missing	estimate of reproductive success
2 - 1o	121	6	5.o	o.95o
11 - 22	73	4	5.5	o.945
2 - 22	194	1o	5.2	o.948

Estimates of reproductive success: young per mature female per year.

Table 4. Estimates of the reproductive success of the female hooded seal from three different areas in the North Atlantic.

	n	x	estimate of reproductive success: x/n
Denmark Strait-Jan Mayen (Øritsland 1964)	337	319	o.947
Newfoundland-Labrador (Øritsland 1975)	376	366	o.973
South Greenland (This study)	358	335	o.936
Total:	1o71	1o2o	o.952

n = Total no. breeding cycles

x = Total no. of successful breeding cycles (i.e. presumed prenancies).

Estimates of reprductive success in young per mature female per year.

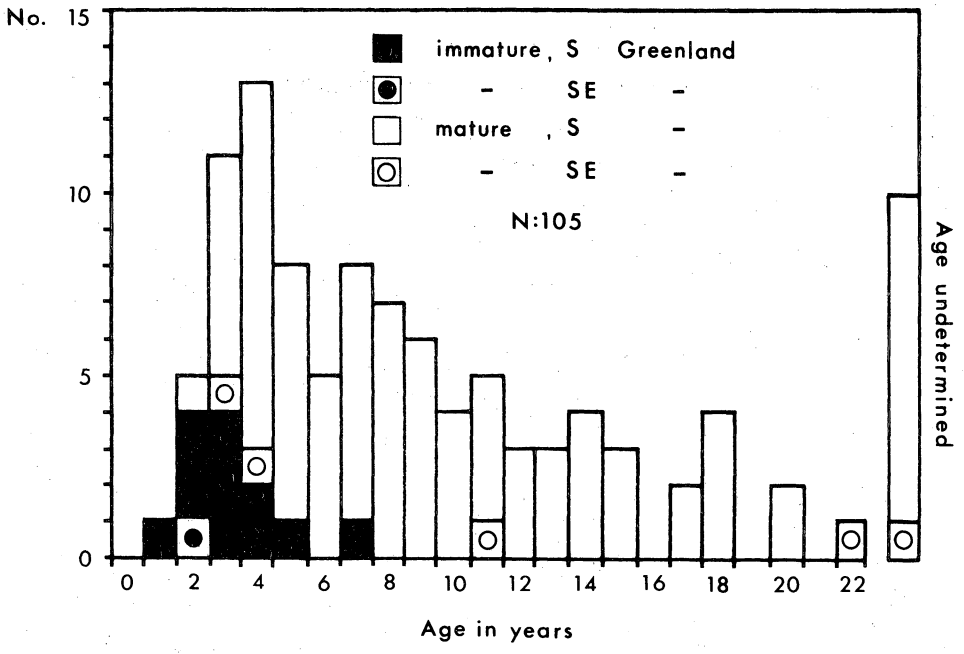

FIG. 1. Composition of a combined sample of female reproductive organs from hooded seals in S and SE Greenland in 1970-71 (20 Apr.- 29 Jul.).

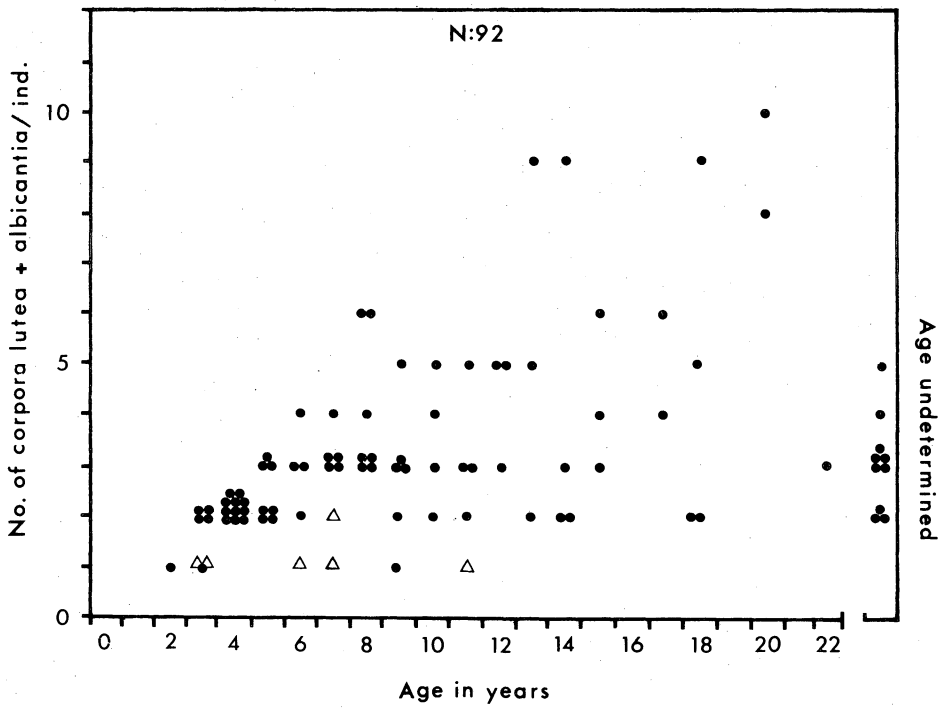

FIG. 2. Accumulation of corpora lutea and albicantia in the hooded seals from S and SE Greenland. Dots : specimens with a corpus luteum; Triangles : specimens only with corpora albicantia.

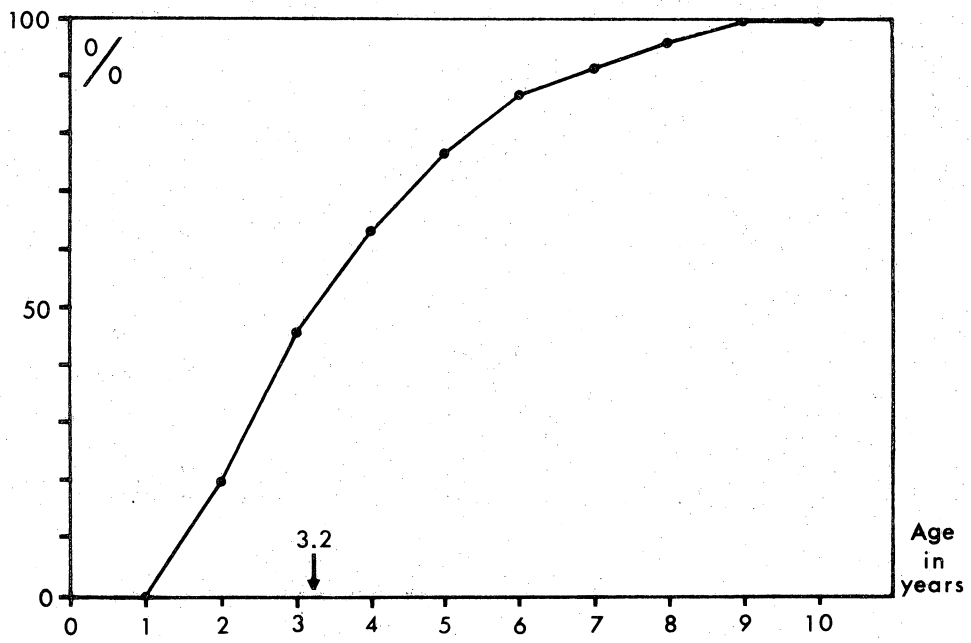

FIG. 3. Accumulated percent of sexually mature female hooded seals in Greenland, (from Table 1, last row).