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Reproduction in the Female Hooded Seal, *Cystophora cristata* Erxleben, at South Greenland

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Abstract

Reproductive organs of 105 female hooded seals, *Cystophora cristata*, from South Greenland in spring and early summer periods of 1970-71, with ages for 95 of the specimens, were used to provide supplementary details on follicular development, corpora lutea and corpora albicantia in the period before attachment of the blastocyst. One instance of implantation of a blastocyst was found in a specimen captured on 29 July. From the distribution of age at first ovulation, the attainment of sexual maturity occurs over age-groups 2 to 9, the median age being 3.2 years and the mean age 4.2 years. The average estimate of reproductive success by three indirect methods was found to be 0.936 young per mature female per year, which is very similar to pregnancy rates reported for hooded seals in other parts of the North Atlantic.

Introduction

Information on the reproductive biology and sexual maturity of the female hooded seal was reported by Popov (1960) for the Greenland Sea in 1956-59 and by Øritsland (1964) for the molting area in Denmark Strait and the breeding area at Jan Mayen in 1956-60. Data are also available on the sexual maturity and reproductive performance of the female hooded seal in the breeding area off Newfoundland and Labrador in 1967-72 (Øritsland, 1975). This paper presents supplementary information on the breeding cycle, sexual maturity and reproductive performance of the female hooded seal at South Greenland in 1970-71 from material collected during their spring migration from the Newfoundland-Labrador area to the molting area in Denmark Strait (Kapel, MS 1972, MS 1974, 1975).

Materials and Methods

As part of the Danish research program on seals at Greenland, lower canines for age determination and reproductive organs were collected from 99 female hooded seals taken at South Greenland (60° N to 61° N) between 20 April and 20 June (six in 1970 and the remainder in 1971). In addition, six female reproductive organs were obtained at Angmagssalik in Southeast Greenland during 18-29 July 1971. Thus, the combined sample of 105 reproductive organs were collected mainly in the period before the attachment of the blastocyst to the uterine endometrium, according to Øritsland (1964). All reproductive organs were fixed and stored in 4% formalin.

In the laboratory, the ovaries were cut into sections about 2 mm thick with a scalpel. The uterine horns were slit longitudinally and transversely to locate the blastocyst. Measurements were made of the volume of the ovaries and the length of the uterine horns along the anterolateral surface from the ovarian bursa to the termination of the horns in the corpus uteri. Two diameters of the uterine horns were measured at their mid-points. All follicles were counted and two diameters of the largest follicle, the corpus luteum and all corpora albicantia were recorded.

Ages were available for 95 of the specimens, as determined by analysis of the cementum growth layers of the lower canines (Kapel, MS 1972; 1975). The remaining 10 reproductive organs without known ages were included in age-independent descriptions of the gross anatomical structures of the reproductive organs. The age composition of the combined sample (Fig. 1) indicates under-representation of the youngest age-groups.

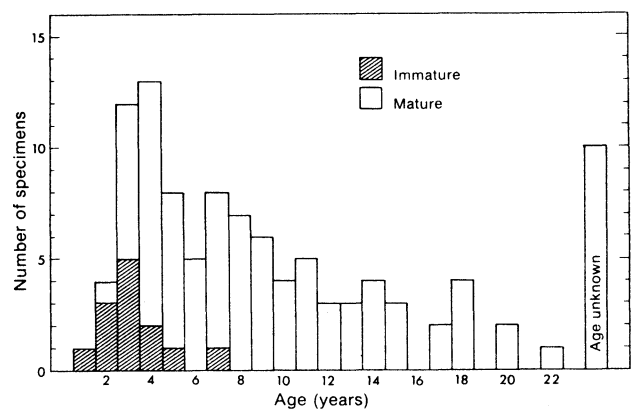

Fig. 1. Age composition of a sample of female hooded seals from South Greenland, 1970-71, collected during 20 April-29 July for reproductive studies.

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Results

A detailed description of the breeding cycle and the gross anatomy of the ovaries of the female hooded seal in the period before the attachment of the blastocyst has been given by Øritsland (1964), and therefore only supplementary details are given in this paper.

Uterine horns and ovaries

Three phases of growth were observed in these organs. There is an age-related phase of growth of the uterine horns and the ovaries to about age 5 years followed by a less pronounced increase in size to about age 22. Imposed on this pattern of growth is an increase in size of the reproductive organs in connection with attainment of sexual maturity (i.e. first ovulation). From this stage, there is a cyclic change in size which is related to the function of the ovaries and the uterine horns in the annual breeding cycle. Øritsland (1964) reported a similar pattern of growth for the female hooded seal, and this seems to be characteristic of most seals (e.g. Hewer, 1964; Smith, 1973).

The post-partum changes in the uterine horn are recognizable as increased diameter of the horn and hyperaemia of the myometrium and the endometrium for about 3.0–3.5 months. This feature is important in deciding whether the large corpora lutea belong to successful pregnancies in the preceding breeding cycle or are regressing corpora lutea of ovulation (i.e. unsuccessful ovulation) in the current breeding cycle. The average diameter of the uterine horns showing post-partum changes was 23.1 ± 4.78 mm (mean and standard deviation) and the average diameter of the other horns was 20.8 ± 4.83 mm, the difference being highly significant ($P < 0.01$, $t = 3.13$, $df = 162$).

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

Follicles

Because of the scarcity of ages 1 and 2 specimens, little can be said about follicular stimulation in association with approaching sexual maturity. However, except for three specimens with no macroscopically visible follicles (one being age 1), the ovaries of immature animals contained about 50 follicles on the average (mean 49,4, range 2–119, standard deviation 41.4, number of animals 20). The large variation in the number of follicles observed in the South Greenland specimens was also noted by Øritsland (1964) and appears to be common for most seals during the same period of the breeding cycle (e.g. Pearson and Enders, 1951; Fisher, MS 1954; Craig, 1964).

During the 20 April–29 July period, there was a decrease in the average number of follicles in ovaries containing the new corpus luteum from about 25 to 17 per ovary. The average number of large follicles remained constant but the number of follicles smaller than 3 mm in diameter declined. As suggested by Øritsland (1964), this change may reflect the increasing hormonal activity of the corpus luteum. In ovaries where the corpus luteum of the preceding breeding cycle (now called corpus albicans) was regressing, the average number of follicles was about seven per ovary, indicating that the regressing corpus luteum retains its follicle-depressing effect for at least 3.0–3.5 months post-partum, as already observed by Øritsland (1964). During the entire period of sampling, there was no trend in the average size of the largest follicle in either of the ovaries.

Follicles larger than 10 mm in diameter were found in 25 specimens. Of these, two were immature with follicles of 12.7 and 11.6 mm in diameter. These animals (aged 2 and 3 years) were approaching sexual maturity, whereas some of the follicles in the remaining specimens (all mature) had reached the preovulatory size (diameter 13.1–15.6 mm) but had apparently been prevented from ovulating by the new corpus luteum. In a 22-year-old specimen (taken on 18 July), a partly luteinized follicle (diameter 14.6 mm) was associated with an apparently healthy corpus luteum. A similar observation was noted by Smith (1973) for the ringed seal, *Pusa hispida*.

Only a few aberrant follicles were found in the ovaries examined. Several haemorrhagic follicles were observed in the inactive ovary of a newly-mature 3-year-old animal, and several small follicles in the ovaries of an immature 3-year-old and a mature 7-year-old had an orange-colored gelatinous content. These follicles resembled those described by Craig (1964) and Smith (1973) as being depressed during a phase of active growth.

Corpora lutea

There was no macroscopic sign of vascular or connective tissue in 12 of the 84 corpora lutea examined. In the remainder, vascular elements and connective tissue had developed to a varying degree with no apparent relationship to time of capture, and none of the corpora lutea showed evidence of advanced degeneration usually related to regressing corpora lutea of ovulation or pseudopregnancy (Pearson and Enders, 1951; McLaren, 1958a, 1958b, Bigg, 1969). Seven specimens had a fluid-filled antrum or ovulation

cavity in the corpus luteum. The size of these cavities showed no relationship to the time of capture, and in the absence of blastocysts there was no evidence to indicate that these vesicular corpora lutea represented infertile ovulations, as suggested by Øritsland (1964) in his study of hooded seals in Denmark Strait. Similar fluid-filled corpora lutea have been described for normal pregnancies in several other seal species (Pearson and Enders, 1951; Harrison *et al.*, 1952; Craig, 1964; Øritsland, 1970; Born and Kristensen, 1982). In this paper, the fluid-filled corpora lutea found in the South Greenland material are regarded as representing normal pregnancies, as they were all in apparently healthy reproductive organs. The interpretation of these vesicular corpora lutea will affect the estimates of reproductive success based on the presence of corpora lutea in the period before attachment of the blastocysts. Such corpora lutea constituted 9.2% (7 of 76) of those animals of known age from South Greenland.

In the period from 20 April to 29 July, the average diameter of corpora lutea increased by 33% from about 12 to 16 mm. A similar increase in size was observed by Øritsland (1964).

Corpora albicantia

Of 92 sexually mature specimens, 82 had a large corpus albicans associated with a uterine horn which showed post-partum changes. The average diameter of the largest corpora albicantia was 9.3 mm (range 6.0–13.5, standard deviation 1.77). By late July, the aveage size of the largest corpora albicantia had decreased to 7.3 mm (75% of the size in late April), and traces of regressing luteal tissue were still evident among the fibrous tissue. A nearly perfect alternation in the functioning of the ovaries during the annual breeding cycle was noted, with 76 and 77 animals (98.7%) having a new corpus luteum in the ovary opposite the one with the largest corpus albicans. A less perfect alternation was observed in the position of the largest and the second largest corpora albicantia, as 12 of 54 specimens (22%) with more than one corpus albicans in the ovaries had the two largest corpora albicantia in the same ovary. This reflects the varying regression rate of corpora albicantia, making it difficult to separate generations of corpora albicantia from size characteristics alone. The second largest corpora albicantia were connective-tissue cores with mean diameter of 6.3 mm (range 3.0–10.5, standard deviation 1.43, number 54). The size frequency of the remaining (66) corpora albicantia approximates a normal distribution with mean diameter of 6.3 mm (range 3.2–7.1, standard deviation 1.01), thus making it impossible to separate different stages of regression in this group from size or structural features.

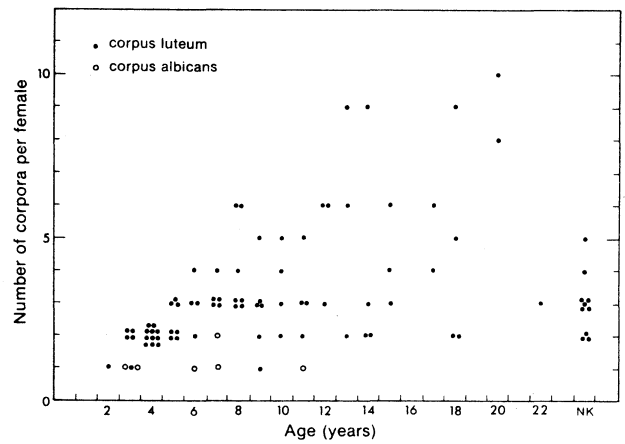

Fig. 2. Distribution of corpora lutea and corpora albicantia in the ovaries of female hooded seals at South Greenland, 1970–71. (NK indicates animals of unknown age.)

The accumulation of corpora lutea and corpora albicantia in the ovaries by age-group (Fig. 2) indicated an increase in number up to ages 7–10 after which the old corpora albicantia appear to be absorbed into the ovarian stroma.

No criteria were found for separating different stages of regessing corpora albicantia into those originating from successful pregnancies and those from infertile ovulations (regressing corpora lutea of ovulation) by structural appearance. This difficulty can be attributed to the fact that the specimens were collected in the early period of the breeding cycle when corpora lutea from infertile ovulations had not yet regressed. However, in seven specimens, the corpora albicantia were associated with immature uterine horns that had not carried any pregnancies, indicating that they were from infertile ovulations. In four animals ovulating for the first time (aged 3, 3, 4 and 6 years), the corpus albicans was the only trace of an ovulation. An age-6 specimen (obtained on 25 May) had a new-looking corpus albicans (diameter 11.7 mm) with regressing luteal elements in one ovary, apparently a regressing corpus luteum of ovulation. Three animals had one corpus albicans in each ovary, both associated with immature uterine horns. One of these animals was 11 years old (killed on 20 April). The similarity of these corpora albicantia of infertile ovulations to corpora albicantia of assumed normal pregnancies during this period of the breeding cycle is therefore confusing. Retention of traces of infertile ovulation for some time may also account for the apparent occurrence of only two corpora albicantia in the same ovary in 6 of the 29 young animals.

Age at sexual maturity

An individual having either a corpus luteum or a corpus albicans in the ovaries was considered to be

TABLE 1. Distribution of age at sexual maturity (first ovulation) for age-groups 1-10 of female hooded seals at South Greenland, 1970-71.

Age (yr)	Total seals	Age at first ovulation 1	2	3	4	5	6	7	8	9	Total mature
1	1	—	—	—	—	—	—	—	—	—	—
2	4	—	1	—	—	—	—	—	—	—	1
3	12	—	6	1	—	—	—	—	—	—	7
4	13	—	2	9	—	—	—	—	—	—	11
5	8	—	1	2	4	—	—	—	—	—	7
6	5	—	—	—	4	1	—	—	—	—	5
7	8	—	—	—	1	5	1	—	—	—	7
8	7	—	—	2	—	1	4	—	—	—	7
9	6	—	—	—	—	1	1	2	1	1	6
10	4	—	—	—	—	—	1	1	1	1	4
Total	68	—	10	14	9	8	7	3	2	2	55
Mature last 3 yr[a]		—	9	12	8	6	5	2	2	2	46
Percent mature		—	19.6	26.1	17.4	13.0	10.9	4.3	4.3	4.3	—

[a] Total of numbers above bars: animals mature within last 3 years.

sexually mature. The method of determining the age at sexual maturity from the numbers of corpora lutea and corpora albicantia was similar to that described fro the hooded seal by Øritsland (1975) and for the harp seal, *Pagophilus groenlandicus*, by Øritsland (1971). In this study, the age determined from tooth cement analysis was considered to be the age at last ovulation, and the maturity analysis was based on three ovarian features, 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 the breeding cycle that ended about a year before capture.

The results of the analysis for age-groups 1-10 are given in Table 1 and the accumulated frequency is shown in Fig. 3. The age at first ovulation ranged from 2 to 9 years. Half of the animals in the sample had experienced first ovulation at an average age of 3.2 years and all older than 9 years were sexually mature. The mean age at first ovulation was 4.2 years (46 animals).

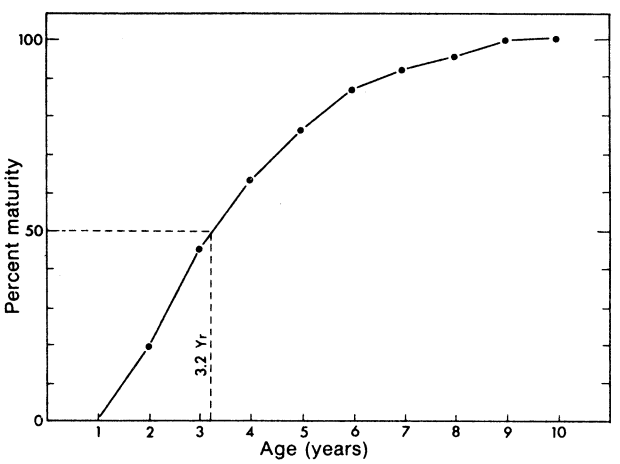

Fig. 3. Accumulated frequency of sexually mature female hooded seals at South Greenland, 1970-71.

Reproductive success

Three different methods of estimating the reproductive success of female hooded seals were applied to the Greenland sample. These methods depended on interpretation of indirect evidence of pregnancy, i.e. the corpus luteum or the corpus albicans. One method, outlined by Øritsland (1971, 1975), involved determining the average reproductive success of annually breeding seals from the numbers of "missing" corpora in an assumed perfectly-alternating sequence of corpora albicantia in individuals. In applying the method to the Greenland material, only corpora lutea and the corpora albicantia from the last three breeding cycles were considered, excluding corpora albicantia associated with ovaries showing no sign of earlier pregnancies. The results of this analysis are given in Table 2 and Table 3 (row 1). Secondly, the presence of an apparently normal corpus luteum, including any with a fluid-filled antrum, was regarded as evidence of a pregnancy, and consequently the ratio of the number of animals with corpora lutea to the number of mature animals in the sample provided an estimate of reproductive success during the current breeding cycle (Table 3, row 2). Thirdly, the presence of a large normal-looking corpus albicans associated with a uterine horn showing post-partum changes was regarded as representing a pregnancy in the preceding breeding cycle, and consequently the ratio of the number of these corpora albicantia to the number of corpora albicantia associated with immature uterine horns or uterine horns showing no post-partum changes provided an estimate of the pregnancy rate (Table 3, row 3).

The average of the three estimates of reproductive success is 0.919 young per mature female per year for age-groups 2-10 and 0.964 for age-groups 11-22, the

TABLE 2. Reproductive performance of female hooded seals at South Greenland, based on missing corpora albicantia in the normal sequence from the ovaries of each animal.

Age group (yr)	Corpora albicantia			Reproductive success
	Total number	Number missing	Percent missing	
2-10	121	6	5.0	0.950
11-22	73	4	5.5	0.945
Total	194	10	5.2	0.948

overall average being 0.936. By the method of Hald (1971), the estimates from the three methods are not significantly different from each other ($\chi^2 = 5.04$, $P > 0.90$ for age-groups 2–10; $\chi^2 = 2.14$, $P > 0.60$ for age-groups 11–22).

Discussion

Øritsland (1975) found no significant difference between the accumulated frequencies of sexually mature female hooded seals from the Newfoundland-Labrador and Denmark Strait-Jan Mayen areas, the latter having been recalculated from data reported by Øritsland (1964). By the Kolmogorov-Smirov two-sample test (Siegel, 1956), the maturity frequencies in this study (South Greenland) do not differ significantly ($P > 0.05$) from either of those given by Øritsland (1975).

Using two different methods of estimating the age at first pupping in hooded seals at Jan Mayen, Jakobsen (MS 1979) found that the mean age at first pupping was about 5 years. The mean age at first ovulation in the sample from South Greenland (this study) was 4.2 years, which indicates that the mean age at first pupping is about 5 years.

The mean estimate of reproductive success of females in the North Atlantic, from Øritsland (1964, 1975) and this study, is 0.952 young per mature female per year (Table 4). None of these estimates for different areas differed significantly ($\chi^2 = 5,82$, $P > 0.90$). The similarity of the three estimates confirms that the reproductive success of the female hooded seal is actually very high and that the pregnancy rate of 0.95 suggested by Øritsland (1975) is realistic for management purposes.

There may be some fallacy in assuming that a break in the normal size sequence of corpora albicantia in an individual indicates that the animal has missed a pregnancy in one of the breeding seasons. Some of the observed differences in the number of corpora albicantia in the two ovaries of an animal may just as well be ascribed to retention of scars from infertile ovulations or to less perfect control of ovulation in young animals. The somewhat higher frequency of "missed" pregnancies in this study than that for lactating females (before the new ovulation) given by Oritsland (1975) may be due to the resorption of corpora from infertile ovulations.

The similarity of the estimates of reproductive success obtained by three methods in this study, with the possibility of excluding some corpora albicantia as originating from definite infertile ovulations, supports the view that average reproductive success may well be estimated from the sequence of corpora albicantia, as suggested by Øritsland (1971, 1975). Furthermore, the similarity of the estimates obtained from examination of corpora lutea and corpora albicantia indicates that the incidence of ovulation serves as a reliable indicator of pregnancy in the female hooded seal.

TABLE 3. Age-specific reproductive success (incidence of ovulations) of female hooded seals at South Greenland, 1970-71, estimated by three different methods.

Age group (yr)	Methods of estimation	Number of breeding cycles (n)	Successful breeding cycles (x)	Reproductive success (x/n)
2-10	Missing corpus albicans	121	115	0.950
	Corpus luteum	55	50	0.909
	Largest corpus albicans	45	38	0.844
	Total	221	203	0.919
11-22	Missing corpus albicans	73	69	0.945
	Corpus luteum	27	26	0.963
	Largest corpus albicans	37	37	1.000
	Total	137	132	0.964
2-22	Missing corpus albicans	194	184	0.948
	Corpus luteum	82	76	0.927
	Largest corpus albicans	82	75	0.915
	Total	358	235	0.936

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

Region	Number of breeding cycles (n)	Successful breeding cycles (x)	Reproductive success (x/n)
Denmark Strait-Jan Mayen (Øritsland, 1964)	337	319	0.947
Newfoundland-Labrador (Øritsland, 1975)	376	366	0.973
South Greenland (This study)	358	335	0.936
Total	1,071	1,020	0.952

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