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Lowered reproductive capacity in female ringed seals (Pusa hispida) in the Bothnian Bay, northern Baltic Sea, with special reference to uterine occlusions

Eero Helle

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The reproduction of female ringed seals, *Pusa hispida* (Schreber), was studied in 225 specimens trapped with seal nets in October-November at Simo, on the northern Bothnian Bay (65°35'N, 25°00'E), and 28 specimens shot on the ice of the Bothnian Bay in April-May, 1973—79.

The ovulation frequency in mature specimens was 0.984. The sizes of the *corpora lutea* and *c. albicantia* were not dependent on maternal age. The *c. luteum* of the pregnant females was larger on average than the regressing *c. luteum* or *c. albicans* of the non-pregnant females in October-November, some 4 months after implantation.

The proportion of normal pregnant females averaged 28 %, decreasing from a maximum of 52 % in the group aged 7—8 years to 8 % in the females over 25 years of age. Females with normal ovulation but no macroscopic uterine signs of pregnancy, i.e. a missed pregnancy, were almost as common, reaching a maximum of 68 % among the newly matured females aged 5—6 years, and averaging 23 % thereafter. An average of 42 % had an occlusion in one or both of the uterine horns, the proportion of both single (26 %) and bilateral occlusions (16 %) increasing with age. This membranous occlusion sealed up the uterine tract, forming a closed chamber with varying amounts and types of fluid. The average position of the occlusion was just over 60 mm from the tip of the horn, ranging from near the tip to the bifurcation. Other reproductive failures averaged 5 %.

Major changes took place in the reproductive status even during the period 1974—79, with the proportion of pregnant females dropping from over 30 % to under 20 % and cases of occlusion increasing from 35 % to 59 %. The numerous reproductive failures, possibly linked with hormonal imbalance and/or severe infections, at present form the most serious threat to the future of the Baltic seal populations.

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1. Introduction

The ringed seal (*Pusa hispida* (Schreber)) in the Baltic Sea is a relict from the Yoldia Sea, a subarctic marine phase of the Baltic Sea some 9000—12000 years ago (Müller-Wille 1969, Curry-Lindahl 1975). Today, the Baltic, a cool, oligohaline sea (salinity 2—7 $^0/_{00}$), is also inhabited by two other species, the grey seal (*Halichoerus grypus* Fabr.) and the harbour seal (*Phoca vitulina* L.). The Baltic seal populations have decreased markedly during recent decades (e.g. Hook & Johnels 1972, Söderberg 1975, Helle 1980b), mostly because of excessive hunting (Söderberg 1975, Helle 1980b) and reproductive disturbances (e.g. Olsson et al. 1975, Helle et al. 1976a, 1976b, Olsson 1977). The reproductive biology of the Baltic seals is still poorly known, for no comprehensive studies were carried out before the 1970s, and only short communications on the ringed seals of the Bothnian Bay have been published in the course of the present study (Helle 1975, Helle et al. 1976b, Helle 1978).

Several extensive studies have been carried out elsewhere on the reproductive biology of pinnipeds (e.g. Enders et al. 1946, Amoroso & Matthews 1952, Harrison et al. 1952, Rand 1955, Amoroso et al. 1965), and a wealth of data exists on phenomena typical of pinnipeds, e.g. delayed implantation (e.g. Harrison 1963, 1964). Almost all the surveys published so far have concerned populations with a more or less undisturbed reproductive status; hunting is the only human activity that places any marked strain upon the stocks.

The purpose of the present paper is to describe the reproductive status of female ringed seals in the Bothnian Bay, and the changes that have taken place over the period 1973—79. Special attention has been paid to reproductive failures, which are common in the population in question.

2. Material and methods

A total of 225 mature female ringed seals were trapped with seal nets in October-November 1973—79 off Simo, a commune on the northernmost part of the Bothnian Bay (65°35'N, 25°00'E) (Fig. 1). The nets (mesh circumference 66 or 80 cm) were 1.5—5 km from the coastline at water depths of 5—10 m; they were anchored to the bottom so that the seals entangled in them soon drowned. For more details of this trapping method see Helle (1979).

This trapping method is selective towards sexually mature ringed seals (Helle 1979), but there is no reason to suppose any bias towards specimens with reproductive failures. Trapping with seal nets has been practised in the Simo area of the northern Bothnian Bay for several decades, the annual catch in 1965—75, for instance, having averaged 175 specimens (max. 577 specimens in 1961; bounty statistics from the Finnish Ministry of Agriculture and Forestry). Since a population inhabiting quite a small area would not have been able to withstand this pressure without a severe decline in numbers, it is highly probable that the ringed seals trapped at Simo had gathered from a larger area (Helle 1979). Reproductive disturbances are also common in females shot in different parts of the Bothnian Bay in spring, and thus it seems likely that the present results and discussion on reproduction in the female ringed seal apply to the whole Bothnian Bay (see Fig. 1).

Another 28 females were shot on the ice in April-May, 1974—79, in different parts of the Bothnian Bay.

The age of each seal was determined from the canine tooth cementum or dentine (Scheffer 1950, Laws 1952); the method has been described in detail earlier (Helle 1979). The mean age in the autumn sample was 15.0 years (*SD* = 6.5, range 5—37) and in the spring sample 14.5 years (*SD* = 8.1, range 5—34).

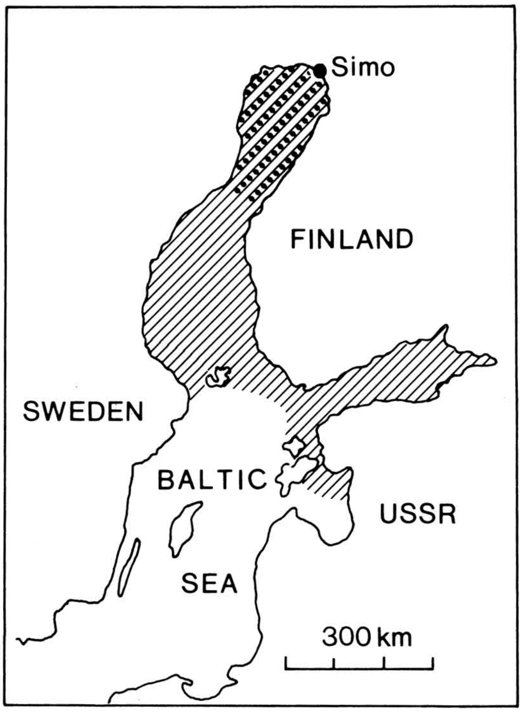

Fig. 1. Study area. The autumn samples originate from Simo and the spring samples from different parts of the Bothnian Bay (dotted). Distribution of the ringed seal in the Baltic Sea (hatched) according to Siivonen (1974).

The ovaries were sectioned transversely at about 2 mm and studied for follicles over 3 mm in diameter and for *corpora albicantia* and *c. lutea.* For the two former the average diameter was measured to the nearest 0.1 mm and calculated from the two extreme measurements on the cut surface, and in the case of the *c. lutea* the third dimension was also included in the average size.

The thickness of the uterine wall was measured to the nearest 0.1 millimetre. Foetuses were sexed, measured (nose — hind flipper) to the nearest millimetre and weighed to the nearest gram. The position of any uterine occlusions was measured from the tip of the horn. The amount of uterine fluid was scored in four classes, and the type was observed.

3. Results

3.1. Uterus

3.1.1. Females with normal pregnancy

Description. In the ringed seal ovulation takes place in the Baltic in February-April (Olofsson

1933, Siivonen 1974, Curry-Lindahl 1975), so that by the present trapping season in October-November the pregnancies had lasted for 6—8.5 months, including a delay of 2.7—3.5 months before implantation (McLaren 1958, Smith 1973). Ringed seals give birth to only one pup a year (e.g. Olofsson 1933, McLaren 1958, Smith 1973). The body length of the normally developed foetuses was in the range 290—510 mm (mean 378 mm, N = 47) by October-November and the weight in the range 510—1995 g (mean 1050 g, N = 47) (see Fig. 2). The foetus was always on the same side as the *corpus luteum*. In the pregnant females the resting uterine horn was generally open, being sealed by an occlusion only in one female caught in October. The uterine wall becomes thinner as it stretches in the course of foetal growth (Table 1). No statistical difference in foetal body size existed between the sexes. The sex ratio of the foetuses was 1:1 over the period 1974—79 (51.8 % males, N = 56).

Occurrence. The pregnancy rate among ovulated females averaged 28.2 % in 1974—79 (Fig. 3), decreasing from a maximum at the age of 7—8 years to only 7.7 % in females over 25 years old. The newly matured females, aged 5—6 years, had a pregnancy rate of only 14 %. The youngest pregnant female was 5 years old, and the oldest 28. Only one twin pregnancy was observed in the autumn sample (mother 20 years old).

The proportion of pregnant females decreased during the period studied ($X^2 = 4.21$, $P < 0.05$), the average decrease being approximately 4 percentage units per year (Fig. 3).

3.1.2. Females with normal ovulation but no macroscopic uterine evidence of pregnancy

Description. This category includes females with a regressing *corpus luteum* or *c. albicans*, indicating normal ovulation during the previous mating season, but with no uterine signs of pregnancy. The uterine wall was thick (Table 1) and longitudinally grooved, as in a quiescent uterus (Fig. 7A). A transverse, membrane-like, constricting scar was observed in the uterine horn in 11 females (Fig. 7B).

Occurrence. Females of this category were almost as common as pregnant ones (Fig. 3), the frequency being highest in the newly matured specimens (5—6 years of age), and in older females averaging 22.5 %. The frequency did not change during the period studied.

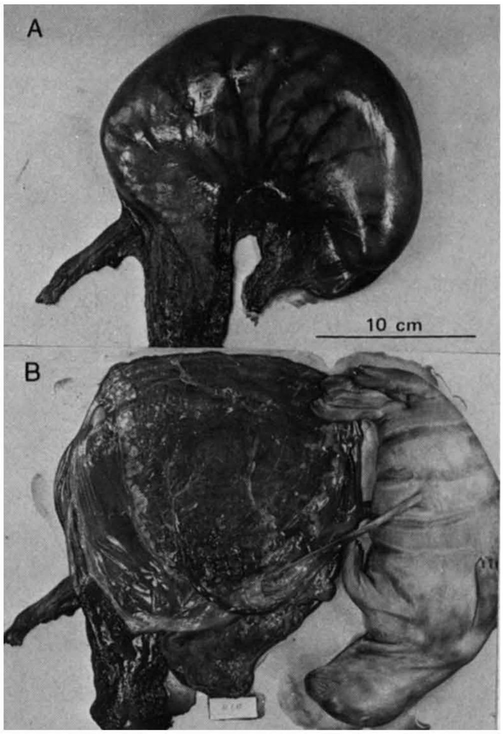

Fig. 2. Unopened (A) and opened (B) uterus of a normal pregnant ringed seal from the Bothnian Bay in October. Note the thin uterine wall. Age of the mother 15 years.

3.1.3. Females with uterine occlusions

Description. This category includes females with an occlusion in one or both of the uterine horns. The occlusion, which generally consists of a thin membrane of connective tissue (Figs. 5B, 6B and 7), forms a closed chamber in the uterine horn, blocking the reproductive tract completely (Figs. 4, 5 and 6). Only in two uteri was the stricture partly open, allowing the escape of liquid from the tract. The small chambers could

Table 1. Thickness of the uterine wall (mm) in uteri of different types in mature ringed seals caught in the Bothnian Bay in October-November.

Type of uterus	N	Mean±SD	Range
Pregnant horn	10	1.70±0.49	1.2—2.8
Normal quiescent horn	47	3.35±0.92	1.3—5.7
Occlusion chamber	29	2.23±0.76	1.0—4.5
in one horn	17	2.12±0.82	1.0—4.5
in both horns			
same side as *corpus luteum*	6	2.00±0.61	1.1—2.8
opposite to *corpus luteum*	6	2.75±0.49	2.5—3.6

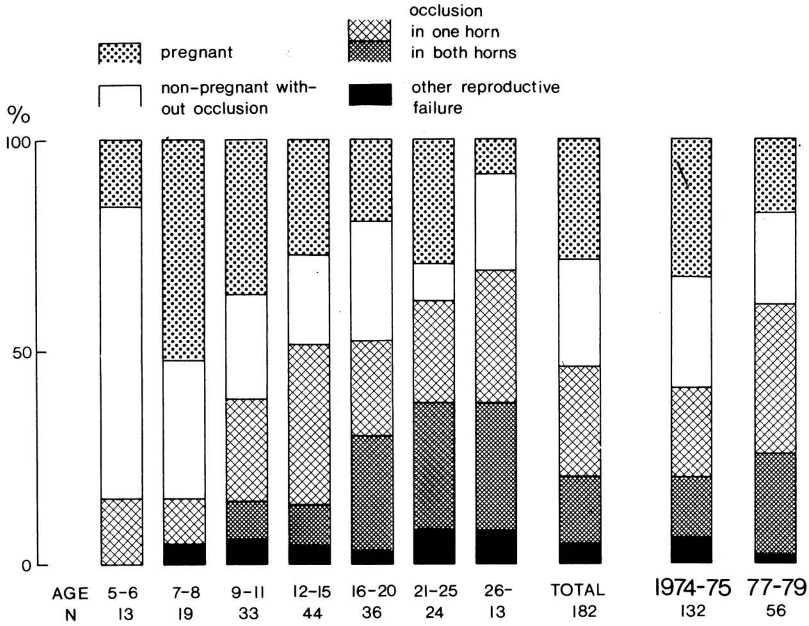

Fig. 3. Reproductive status of ovulated ringed seals by age and by two trapping periods in the Bothnian Bay, 1974—79.

not be detected externally, and the empty chambers could not be felt by palpation in unopened uteri, whereas the larger chambers were easy to detect externally (Fig. 4).

The occlusion was situated at an average distance of 61.1 mm ($SD = 21.0$, range 20—114, $N = 63$) from the tip of the uterine horn, the lowest position being in the trunk of the uterus near the bifurcation (Fig. 7B). The width of the chamber averaged 29.2 mm ($SD = 15.2$, range 8—75, $N = 62$), exceeding the average width of a quiescent horn (Helle 1977). No difference in the size of the chambers was found between the singly and bilaterally occluded uteri. In one case two occlusions occurred in the same horn, separated by a distance of 15 mm.

The thickness and appearance of the uterine wall surrounding the chamber varied greatly (Tables 1 and 2). It tended to be thicker than in the pregnant horns, but thinner than in the quiescent ones. At its most typical the uterine wall was extremely thin (< 2 mm), smooth and sometimes fibrous on its inner surface (Figs. 5 and 7). Sometimes the uterine wall surrounding the chamber took the appearance of a longitudinally grooved quiescent horn. When these extreme types were encountered in the same chamber the longitudinally grooved part always occurred at the upper end of the horn (Fig. 6B).

The amount and nature of the fluid in the chamber varied considerably. It was often light brown, turbid and foul-smelling, with decomposing particles floating in it, but sometimes reddish-brown, clear and odourless. Intermediate types were frequent.

A correlation was found between the amount and nature of the fluid and the thickness and the appearance of the uterine wall (Table 2). The wall was typically very thin in chambers containing copious and relatively turbid pus, while those containing little or no fluid, often clear in appearance, had thicker and usually at least partly longitudinally grooved walls.

Occurrence. An average of 25.5 % of the mature females suffered from an occlusion in one horn and 16.5 % in both horns in 1974—79. A single uterine occlusion reached its highest rate among females aged 12—15 years and a bilaterally occluded uterus in those over 25 years of age (Fig. 3). The proportion of occluded uteri increased with age, exceeding 57 % in the females over 20 years. The youngest female with a single occlusion was 5 years old and the youngest with bilateral occlusion 7. Both were observed in the spring of 1979. The mean age of the females with a single occlusion was 15.3 years and of those with bilateral occlusion 18.4 years ($t = 2.23$, $P < 0.05$),

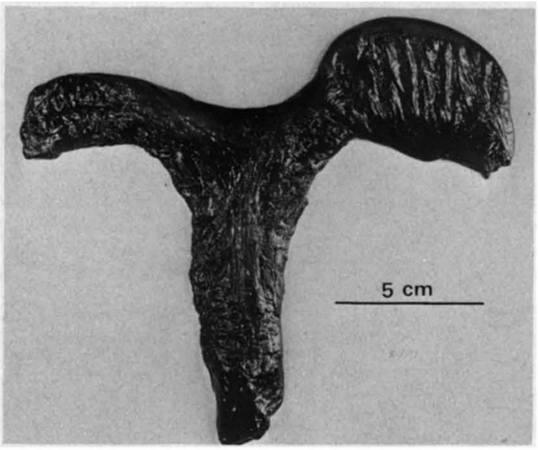

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Fig. 4. Uterus with a large, clearly detectable occlusion chamber in one uterine horn. Age of the seal 22 years.

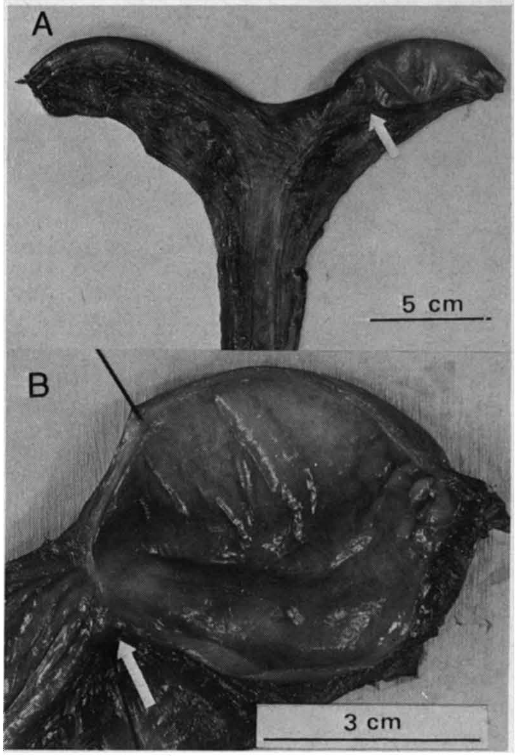

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Fig. 5. Typical occlusion chamber in a 15-year-old ringed seal from the Bothnian Bay. A. Unopened uterus, B. Occluded horn opened. The arrow indicates the position of the occlusion. Note the smooth, thin wall within the occlusion chamber and the thicker, longitudinally grooved wall outside it (cf. Fig. 6).

and neither value decreased during the study period.

The proportion of females with uterine occlusions had increased from 34 % in 1974—75 to 59 % by 1977—79 ($X^2 = 9.36$, $P < 0.01$) (Fig. 3). This is not explained solely by the increase in the mean age of the catch (see Helle 1980a).

3.1.4. *Females with other kinds of reproductive failure*

Description. Five females showed signs of abortion or resorption, namely a dilated uterine horn and/or decomposing remnants of placenta

Table 2. Thickness and macroscopic structure of the uterine wall and the nature of the uterine fluid in relation to its amount in female ringed seals in the Bothnian Bay in October-November.

Amount of uterine fluid (0—3)	Thickness of the uterine wall (mm)					Quality of the inner surface of the uterine wall				Nature of the uterine fluid		
							smooth	grooved				
								in part of chamber	all round the chamber			
	N	1.1-2.0	2.1-3.0	3.1-4.0	4.1-5.0	N				N	turbid	clear
Copious (3)	3	2	1			10	10			7	5	2
Moderate (2)	5	1	4			10	9	1		3	2	1
Little (1)	15	4	8	2	1	18	10	8		9	2	7
None (0)	4		1	1	2	8	1	2	5			
Total/Mean	27	1.7	1.4	0.7	0.3	46	1.9	0.9	0.0	19	2.3	1.5

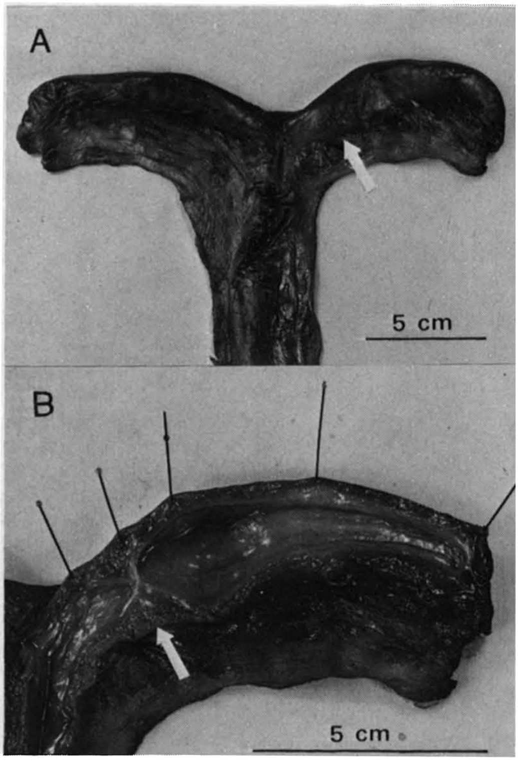

Fig. 6. Occluded uterine horn of a 19-year-old ringed seal from the Bothnian Bay. A. Unopened uterus, B. Occluded horn opened. The arrow indicates the position of the occlusion. This thick-walled occlusion chamber (cf. Fig. 5) contained only a little fluid. Note the upper end of the chamber, where longitudinal grooves can be detected in the uterine wall.

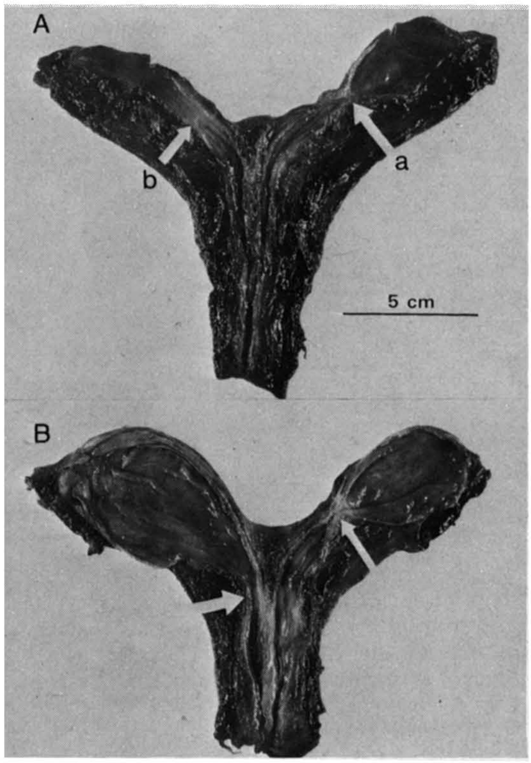

Fig. 7. Special cases of occluded uteri. A. Opposite to a typical occlusion (a) a membrane-like constricting scar (b) can be seen in an unclosed, thick-walled uterine horn (cf. Fig. 6B). Age of the seal 22 years. B. Uterus of a 29-year-old ringed seal from the Bothnian Bay with occlusions (arrows) in both horns, one situated near the bifurcation of the tract. Both chambers were thin-walled with a smooth inner surface.

or foetal membranes. In another four females foetal development was markedly retarded and it was impossible to determine whether the foetuses had been dead or alive at the moment of trapping, although macroscopically they seemed to be in good condition. The lengths of the foetuses were 25, 35, 59 and 195 mm, and in the last three cases the outer length of the enlargement of the uterine horn was 107, 113 and 145 mm (cf. the sizes of the occlusion chambers). The foetal lengths suggest that development was retarded by almost 3 months in the first three cases (see Smith 1973).

Occurrence. The frequency of this category averaged 4.8 % and did not change during the period studied (Fig. 3).

3.2. Ovaries

3.2.1. Follicles

The mature female ringed seals had an average of 13.7 follicles over 3 mm in diameter (Table 3), with no differences between the reproductive categories. Follicular activity decreased after 20 years of age, and inactive ovaries were found in all reproductive categories. The mean size of the largest follicle varied from 4.3 mm in the females with bilateral occlusion to 5.7 mm in pregnant females in autumn. No statistical differences were found.

The site of the largest follicle showed no relation to the position of the *corpus luteum* in October-November, occurring with equal frequency in conjunction with it and opposite to it.

Table 3. Number of follicles over 3 mm diameter in female ringed seals by reproductive status and by age in the Bothnian Bay in October-November.

Reproductive status	*N*	Mean±*SD*	Range	Age in years	*N*	Mean±*SD*	Range
Pregnant	56	13.8±6.7	0—27	—10	47	12.3±6.5	0—25
Non-pregnant without occlusions	40	11.6±6.6	0—20	11—15	48	14.5±7.6	3—29
Occlusion in one horn	41	14.9±9.3	0—35	16—20	36	17.1±8.1	0—36
Occlusion in both horns	26	15.1±8.4	0—36	21—	32	10.8±7.9	0—21

3.2.2. *Corpus luteum*

The size of the *c. luteum* (excluding accessory ones) averaged 13.6 mm in autumn and was not dependent on maternal age (Table 4). The mean size of the *c. luteum* in spring reached 11.6 mm (SD = 1.0, range 9.8—13.2, N = 13), and no differences were observed between the reproductive categories. Three evidently mature females (12—15 years of age) had not ovulated during the previous mating season, the ovulation frequency for the whole material thus being 0.984 (N = 191). One female carried two *c. lutea*, one in each ovary, maintaining a twin pregnancy in October-November. No cystic *c. lutea*, luteal cysts or follicular cysts (see Roberts 1971) were found.

3.2.3. *Corpus albicans*

The regressing *c. luteum* or *c. albicans* was of approximately the same size in the different reproductive categories (Table 4), being significantly smaller than the *c. luteum* of pregnancy in autumn (t = 5.30—10.05, in all $P < 0.001$). The size of the *c. albicans* was not dependent on the age of the seal. It is worth noting that all categories contained some *c. lutea* of ovulation/*c. albicantia* that were even larger than the average *c. luteum* of the pregnant females (Table 4). The macroscopic appearance varied from totally healthy-looking *corpora* to those carrying whitish scar tissue in process of formation from the centre outwards.

A *c. albicans* originating from ovulation about 19 months earlier was clearly visible in 15 % of the mature females in autumn. These were obviously associated with pregnancies which had led to normal parturition 7—8 months before sampling. The mean size of these was 4.4 mm (SD = 1.0, range 2.9—7.4 mm, N = 43). In spring the *c. albicantia* originating from parturition 1—2 months earlier averaged 6.5 mm (SD = 0.8, range 5.6—7.5 mm, N = 4).

3.2.4. *Activity of ovaries*

Ovulations were distributed evenly between the ovaries, as also were the foetuses, occlusions and other reproductive failures in the uterine horns (Table 5).

Table 4. Size of *corpus luteum* and most recent *c. albicans* (mm) in the various reproductive categories and age-classes of female ringed seals in the Bothnian Bay in October-November.

Reproductive category		Age in years —10	11—15	16—20	21—	Total
Pregnant	mean±*SD*	13.7±2.1	13.4±2.1	13.6±1.3	13.4±1.9	13.6±1.9
	N	23	15	12	9	59
	range	9.1—16.4	10.9—16.0	11.3—15.5	11.9—17.2	9.1—17.2
Non-pregnant without occlusions	mean±*SD*	9.4±2.1	9.9±1.3	10.8±1.3	9.1±1.7	9.8±1.8
	N	19	9	9	4	41
	range	4.6—13.0	7.7—11.9	7.0—12.2	7.9—11.6	4.6—13.0
Occlusion in one horn	mean±*SD*	10.3±1.6	9.6±2.5	9.9±2.1	8.7±2.4	9.6±2.3
	N	7	18	7	8	40
	range	7.6—12.5	4.9—13.4	5.8—12.3	6.4—13.8	4.9—13.8
Occlusion in both horns	mean±*SD*	12.9	7.5±3.3	10.3±1.9	10.1±1.7	9.9±2.3
	N	1	4	10	10	25
	range		6.0—11.4	6.1—12.7	7.6—12.8	6.1—12.8
Pregnancy disturbed in some other way	mean±*SD*	10.1	11.5±2.3	11.4±3.4	7.9±2.5	9.9±2.8
	N	1	3	2	4	10
	range		8.9—13.2	9.0—13.8	3.7—10.1	3.7—13.8

Table 5. Position of foetus, occlusion and other reproductive failure on the two sides of the uterus, and position of *corpus luteum* in the two ovaries of non-pregnant ringed seals in the Bothnian Bay in autumns 1973-78 (no differences in X^2-test).

	Right		Left	
	N	%	*N*	%
Foetus	33	57.9	24	42.1
Occlusion	25	55.6	20	44.4
Other reproductive failure	3	33.3	6	66.7
c. luteum in non-pregnants	24	57.1	18	42.9

4. Discussion

4.1. Ovarian activity

As judged from the presence of the *corpus luteum* or absence of the Graafian follicle, fecundity in pinnipeds varies greatly between species, from 0.61 in the leopard seal (*Hydrurga leptonyx*) in the Antarctic (Øritsland 1970) to 0.988 in the hooded seal (*Cystophora cristata*) in the northwestern Atlantic (Øritsland 1975) and in the ringed seal in Canada (Smith 1973). The present figure of 0.984 for the Baltic ringed seal is high as compared both with other species and with values for the ringed seal elsewhere.

The ovulation frequency also varies within one species depending on physiological and ecological factors, e.g. on hunting pressure (Sergeant 1966, Nazarenko & Beloborodov 1974). Söderberg (1978) found a drop of 2.0 years in attaining sexual maturity in Baltic ringed seals during 1936—68, and the Bothnian Bay ringed seals suffered from excessive hunting in the mid-1960s (up to 1967) (Helle 1980b). Hunting pressure and the decline in reproductivity (as shown here) may account for the extremely high ovulation frequency sustained. Double ovulations leading to twin pregnancies (one case in the present material) are rare in pinnipeds, but have been recorded occasionally (e.g. Scheffer & Slipp 1944, Stirling 1967).

Macroscopic observations on the ovaries suggest that in the ringed seals of the Bothnian Bay population ovulation frequency is high and quite normal.

4.2. Ratios of the reproductive categories

Pregnancy rates are usually about as high as ovulation frequencies, 94 % of the mature females in a harbour seal population being pregnant (Boulva & McLaren 1979), and 93 % near term pregnancies being observed in the harp seal (*Pagophila groenlandica*) (Sergeant 1966) and 87 % in the crabeater seal (*Lobodon carcinophagus*) (Øritsland 1970). In ringed seals the pregnancy rates vary from 63 % on Choska Inlet (Nazarenko 1964) to 85 % in the Sea of Okhotsk (Fedoseev 1975). The present pregnancy rates are lower than have been observed anywhere in pinnipeds. It must further be noted that the present pregnancy rates were recorded some 3—4 months before the pupping season and hence the birth rates may in fact be even lower than these. The low number of clearly visible *c. albicantia* originating from the previous breeding season is indicative of this.

Young pinniped females do not always become pregnant in their first year/years of maturity (McLaren 1958, Kuzin 1978), as was also noted in the present material, but non-pregnant females averaged 20—25 % among those aged over 8 years. It is noteworthy that these females had ovulated, whereas the non-pregnant harp seal females in the White Sea (23 % on average), for instance, had not ovulated (Nazarenko & Beloborodov 1974).

The history of non-pregnant females without occlusions is obscure. At the present sampling time, 7—8 months after fertilization, the methods used could not have detected any signs of resorption that may have occurred during the delay period or just after it (0—4 months after fertilization). Even the size of the regressing *c. luteum* or *c. albicans* was not very informative for, although it tended to be smaller than the *c. luteum* in pregnant females, overlapping was common (Table 4). In the harbour seal the *c. luteum* of non-pregnant females may persist for at least 3.5 months without showing much regression (Bigg 1973, Bigg & Fisher 1974), and in the ringed seal no signs of regression are apparent for 5.5 months (Smith 1973). In the ringed seal, in fact, a large *c. luteum* seems to persist for 7—8 months in some cases.

Thus it remains undecided whether the non-pregnant females without occlusions had failed to be impregnated or whether the potential conceptus had suffered from early death and resorption. In any event, the seal had missed a pregnancy (see Craig 1964). In this context it is worth noting that the reproductive performance of males in the area is unknown.

Reproductive failures reached 12 % in a harbour seal population throughout the cycle (Bigg 1969), 3—5 % in the phocids inhabiting the Pacific Ocean (Tihomirov 1966), and locally 20 % in the California sea lions (e.g. Gilmartin et al. 1976). Missed pregnancies, resorptions and abortions have also been reported in the northern fur seal (*Callorhinus ursinus*) (Pearson & Enders 1951), South African fur seal (*Arctocephalus pusillus*) (Rand 1955) and elephant seal (*Mirounga leonina*) (Laws 1955). The present proportion (4.8 %) of disturbances other than missed fertilizations or implatations and occluded uterine horns is comparable with these figures. The increasing frequency of occluded uterine horns, the chief cause of reproductive failure in the present Bothnian Bay population, appears to be unique and so cannot be compared with any findings elsewhere. The condition was already recognized by 1973, and a retrospective study has detected the first signs of lowered reproductivity in the late 1960s (Helle 1980b).

4.3. Uterine occlusions

The present uterine occlusions have certain features in common with hydrometra and mucometra (see e.g. Jubb & Kennedy 1963, Roberts 1971). In long-standing cases of mucometra the uterine walls are thin and fibrosed (Jubb & Kennedy 1963, Roberts 1971), and earlier information on the pus accumulating in the uteri in farm animals with its typical colouring and pungent odour (Roberts 1971) also fits with the present uterine pathology (Table 2). In farm animals with hydrometra or mucometra infection of the uterus results in an intractable pyometra, with normal ovaries but permanent sterility (Jubb & Kennedy 1963).

Most cases of pyometra in the bitch are due to prolonged hormonal imbalance (Jubb & Kennedy 1963, Roberts 1971), and according to Roberts (1971) the inflammatory reaction of endometritis and pyometra is progesterone-dependent. It is further known that the uterus is especially susceptible to infections when under the influence of progesterone at any time, including pregnancy (Jubb & Kennedy 1963, Roberts 1971).

Pyometra is usually a sequel of a uterine infection or the early death of an embryo, or both (Roberts 1971). Thus purulent pyometra with a copious foul-smelling discharge has been produced by introducing *Escherichia coli* (Lynn 1965). In pinnipeds *Leptospira pomona* (Smith et al. 1974, Sweeney 1974) and San Miguel Sea Lion virus (Gilmartin et al. 1976) are known to cause premature births, but not disturbances at an early stage of foetal development.

The reason for the present occlusion is not known, only its dependence on the age of the seal (Fig. 3). However, a correlation has been reported between reproductive failures in Baltic seals and high levels of PCBs and DDT, and it has been suggested that uterine occlusions may at least partly be due to high levels of PCBs (Helle et al. 1976a, 1976b, Olsson 1977). PCB and DDT compounds are known to interfere with steroid hormone metabolism (e.g. Kunzman et al. 1966, Conney et al. 1967, Kupfer 1969, Pardini 1971), and to lower resistance to infections (e.g. Friend & Trainer 1970, Hansen et al. 1971), and these hydrocarbons may exert one or both of these effects on the present seal population. PCB and/or DDT are found to have caused abortions in the California sea lion (Gilmartin et al. 1976) and a lowering of reproductive rate in harbour seals in the Wadden Sea (Reijnders 1979).

The position of the occlusions, ranging widely from near the tip of the horn to near the bifurcation, would point to an occlusion formed before implantation and the formation of the foetal membranes. On the other hand, decomposing pieces of placenta and/or embryo, originating from a not very recently dead conceptus, were sometimes found in the pus (see also Roberts 1971). So the probable timing of the disturbance leading to uterine occlusion would therefore be during the delay period or at the very beginning of foetal growth after implantation, in March-July, resembling the situation in pyometra, which usually occurs during the metestrum or pseudopregnancy (Jubb & Kennedy 1963, Roberts 1971). For the present it remains unknown whether the process leading to an occlusion always destroys a conceptus or whether it also takes place in non-pregnant horns.

In bilaterally occluded uteri the older occlusion has been present for at least 19 months, and possibly for much longer. One occluded horn does not affect ovulation on the opposite side, as it does in pyometra (Roberts 1971). The permanence of pyometra depends on the severity of the inflammation (Jubb & Kennedy 1963, Roberts 1971). The present study would indicate that the occlusion may be cured spontaneously, at least in some cases, for a gradual sequence of events may be hypothesized to have begun from thin-walled chambers containing copious, turbid pus with remnants of placenta and foetal membranes towards empty, thick-walled chambers and in the end to an open uterine tract with only a transverse scar in the uterine wall to mark a previous occlusion (see Fig. 7).

Occlusions in uterine horns and disturbances in endometrial function may interfere fundamentally with reproductive function, for a close relationship exists between the function of the endometrium and the ovaries (e.g. Williams 1927). In the pig, for instance, according to Ginther (1966), at least 1/4 of the uterine horn or its endometrial tissue is needed for luteal regression. A scarcity of this tissue may also be caused when the endometrium is destroyed in pyrometra (Ginther 1966). In the present material the endometrium was probably destroyed in most of the occlusion chambers, but the *c. luteum* seemed to have regressed even when associated with a large chamber. There is no evidence of whether this happened at the normal time or later. Nalbandov (1952) observed that in the pig a blind or occluded uterine horn always leads to early embryonic death in the opposite horn, and the same was found in the present ringed seal material, with a single exception.

The high frequency of reproductive failures in the ringed seal population of the Bothnian Bay is very serious, and so is the rapid change in reproductive status during the 1970s. Without exaggeration, it may be stated that, if the situation observed in the Bothnian Bay holds good for the whole of the Baltic, the future of the Baltic seal populations is seriously threatened, unless a radical change for the better takes place in the near future.

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