Decline in the pregnancy rate of Baltic grey seal females during the 2000s

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Kauhala, K., Ahola, M. P. & Kunnasranta, M. 2014: Decline in the pregnancy rate of Baltic grey seal females during the 2000s. — *Ann. Zool. Fennici* 51: 313–324.

During the period 2000–2012 we witnessed a general increase in the Baltic grey seal (*Halichoerus grypus*) population size. Population growth has, however, ceased in the northern sea areas. The accompanying changes to age structure during this time suggest a reduced female pregnancy rate. In this study, we used hunted individuals to examine the ovulation and pregnancy rates of seals from different age classes and years. We examined the presence of *corpus luteum*, *corpus albicans* and placental scars from seals killed before the implantation period and fetuses after the implantation period. The pregnancy rate derived from the presence of *corpus albicans* or placental scars in the pre-implantation period was similar to that based on fetuses. Thirty-three percent of females ovulated at the age of 3 years, 81% at the age of 4 years and 99% thereafter. The pregnancy rate was lower among 4–5-year-old females (0.54–0.56) than among 6–24-year-old females (0.77–0.86), being highest in 7–11-year-old females. The pregnancy rate of 6–24-year-old females decreased from 0.89 in 2000–2004 to 0.66 in 2005–2011 and correlated negatively with population size. The decreased pregnancy rate suggests that grey seal numbers in the northern part of the Baltic Sea may be today close to the carrying capacity of the environment.

Introduction

According to estimates there had been about 100 000 Baltic grey seals (*Halichoerus grypus*) at the beginning of the 20th century but thereafter seal numbers declined and were lowest (about 2000–3000) in the 1970s (Jensen *et al.* 1969, Almkvist 1978, Bergman & Olsson 1986, Kokko *et al.* 1997, Bergman 1999, Harding & Härkönen 1999, Harding *et al.* 2007). One reason behind this dramatic decline was environmental pollution by organochlorines in the 1960s and 1970s,

which likely caused severe reproductive disturbances (Bergman & Olsson 1986, Bergman 1999, Harding & Härkönen 1999, Bäcklin *et al.* 2003, Nyman *et al.* 2003). Due to decreased levels of environmental pollution in the Baltic Sea during recent decades (Routti 2009), reproductive health of seals has gradually improved and in the 2000s, virtually no reproductive disturbances have been observed (Bäcklin *et al.* 2011, 2013a, Roos *et al.* 2012). Accordingly, Baltic grey seal numbers have increased since the 1980s, and in 2012 the number of grey seals
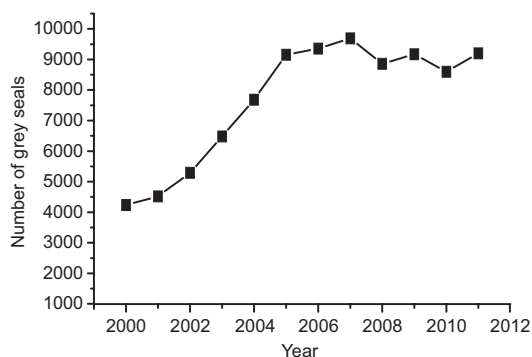
Fig. 1. Numbers of grey seals seen during aerial surveys in late May–early June in the Finnish sea area (Ahola 2014). Values were smoothed with three-year moving averages because of stochastic variation in the numbers of seals seen during aerial surveys.

seen in aerial surveys was about 10 000 in the Finnish sea area and 28 000 in the entire Baltic Sea (Ahola 2014).

The number of counted grey seals in the Finnish sea area increased until the mid-2000s but has fluctuated thereafter (Fig. 1). Furthermore, the demographic structure of the population changed and the mortality rate of especially females under 10 years old increased from the early to the late 2000s (Kauhala *et al.* 2012). The ceased population growth and the increased mortality rate may indicate that seal numbers in the northernmost areas of the Baltic Sea are approaching the carrying capacity of the environment. If this is the case, we can expect a decrease in the pregnancy rate during the 2000s (Begon *et al.* 1986, Harding *et al.* 2007, Svensson *et al.* 2011). It is important to know whether the population is close to carrying capacity when planning seal population management: the number of seals that can be hunted annually depends on the status of the population. Such information may also help to solve the seal-fishery conflict, which has arisen in Finland due to increased seal numbers: if the population has already reached its carrying capacity, more seals can be hunted and damage to coastal fisheries diminishes.

The grey seal is a seasonal and synchronized breeder giving birth to one pup in February or March in the Baltic Sea (Boyd *et al.* 1999). The pup is born on drift ice or on land, if there is no suitable ice available. The lactation period lasts almost three weeks. Seals have a postpartum estrus and spontaneous ovulation: females ovulate and mate at the end of the lactation period, 12–17 days after parturition (Atkinson 1997, Boyd *et al.* 1999). After fertilization there is a period of about 3.5 months when the blastocyst may grow slowly but remains unattached in the lumen of the uterus (Atkinson 1997). Implantation in Baltic grey seals takes place usually in July but sometimes not before early August (Bäcklin *et al.* 2011). The presence of fetuses after the implantation period (i.e. from early August onwards) can thus be used to calculate the pregnancy rate of a female seal population in the present year.

Corpus luteum (CL) is formed within 24 hours after ovulation and secretes progesterone which, with placental gonadotrophins, maintains pregnancy (Boyd *et al.* 1999). CL rapidly atrophies after parturition and changes to *corpus albicans* (CA; Boyd 1983, 1984a). Both the presence of CA and the remains of placental scars, which can often be seen in the uterus after parturition, indicate that the female gave birth in the present year, i.e. was pregnant the previous autumn (Boyd 1984a, 1985).

The reproductive capacity of a seal population is closely linked to population density in relation to the carrying capacity of the environment (e.g. Atkinson 1997), and is therefore essential information to proper management evaluations. The aim of the present study was to use hunted animals from the years 2000–2012 to evaluate the yearly pregnancy rate of Baltic grey seal females of different age groups from the presence of *corpus albicans* and placental scars before the implantation period, and from the presence of fetuses after the implantation period. We also aimed to estimate the ovulation rate of females from the presence of *corpus luteum*. We predicted that the pregnancy rate decreased during the 2000s, because growth rate declined and demographic structure of the population changed in the northern sea areas (Kauhala *et al.* 2012).

Methods

Samples of grey seals were collected from hunters and occasionally from fishermen's by-catch

between 2000 and 2012 from the Finnish sea area including Åland: Bothnian Bay (ICES subdivision area 31), Bothnian Sea and the Quark (ICES SD 30), SW archipelago (ICES SD 29) and the Gulf of Finland (ICES SD 32; Fig. 2). Annually, several hundreds of grey seals are hunted in Finland during the hunting season from 16 April to 31 December (16 April–31 January in Åland). We received 575 samples of females, which were at least two years old. Younger females were excluded from the data since they are likely to be non-fertile (Boyd 1985).

Samples of each female seal included at least the uterus, ovaries and the lower jaw. Seal species was confirmed from the lower jaw. Age determination was done by counting incremental lines in the cementum from transversal sections of lower canine teeth (e.g. Mansfield 1991).

The uterus was first checked for the presence of occlusions or stenoses, then cut open and examined for signs of placental scars or fetuses. We also recorded their location (left or right horn) in the uterus. A fresh scar is like a black belt inside the uterine horn. After some weeks only the rims of the scar can be seen but the horn in question is still thicker at the site of the placental scar than the other horn. Some orange spots may be seen at the site of the placenta (U. Siebert pers. com.).

Due to delayed implantation, we divided the data into 'spring data' (seals killed before the implantation period, i.e. before 1 July) and 'autumn data' (seals killed after the implantation period, i.e. after 1 August). We received 472 females (≥ 2 years old) from spring, mainly from May, from which we could examine the presence of placental scars. The proportion of females with placental scars from the pre-implantation sample should indicate the proportion of females that gave birth in the present year (i.e. pregnancy rate of the previous autumn). Pregnancy rate was also determined from the autumn sample as the proportion of females with fetuses after the period of implantation ($n = 23$). Because not all embryos have implanted or are so small that they cannot be seen in July, pregnancy rate was calculated from females killed after July (Bäcklin *et al*. 2011). Head-body length of fetuses (from nose to flipper) was also measured to calculate a
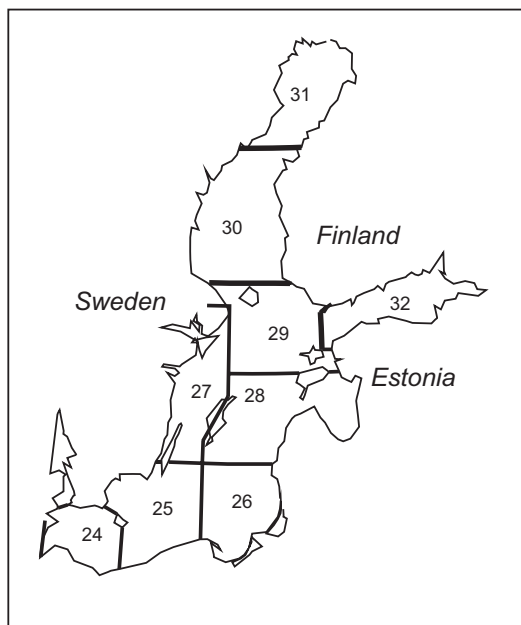

Fig. 2. Grey seal samples were collected from the Finnish sea area from ICES SD areas 29–32. Original map by Kauhala *et al*. (2012).

growth curve for the fetuses (sexes were pooled because the sex of most fetuses was unknown).

Ovaries were removed and cross sections (thickness about 2 mm) were made with a knife. They were examined by eye for the presence of *corpus luteum* (CL) or *corpus albicans* (CA). Both sides of each section were examined for CL (yellowish, soft in texture and occasionally with a hollow center) and CA (whitish in color, scar-like in texture). The positions of CL and CA in the left or right ovary were recorded. Seals usually ovulate from alternate ovaries in successive years (Atkinson 1997, Boyd *et al*. 1999).

We calculated ovulation rate from the spring sample (time period between ovulation and implantation) as the proportion of females with CL ($n = 488$ for ≥ 2-year-old females). CL remains active during the phase of delayed implantation even when a female is not pregnant but regresses in non-pregnant females after the implantation period (or if the embryo dies at an early stage) due to the absence of hormones from the placenta (Boyd 1984a, Boyd *et al*. 1999). Therefore, we did not use the autumn sample to calculate ovulation rate. The lengths of CL ($n = 384$) and CA ($n = 279$) were measured to the nearest mm.

We also calculated the proportion of females that gave birth in the present year (i.e. were pregnant the previous autumn) from the pre-implantation sample as the proportion of females with CA ($n = 471$ for ≥ 2-year old females). CA may persist about one year until the next parturition but may be small after the period of implantation (Hewer 1964). In non-pregnant females, CA disappears after the period of implantation because it needs progesterone and placental gonadotrophins to survive (Boyd 1984a, Boyd et al. 1999). However, as a result of the infertile estrus cycle (the present year), CA may be seen in the autumn, which can be erroneously interpreted as a sign of pregnancy in the previous year (Boyd 1984a). Pregnancy rate in the previous year on the basis of the presence of CA was thus calculated using samples only between ovulation and implantation. We tested, however, difference in pregnancy and ovulation rates between pre-implantation and autumn samples to evaluate whether the autumn samples for CA and CL should indeed be excluded from our data.

To summarize, pregnancy rate was estimated using three methods. Pregnancy rate (year t): (i) the proportion of females with CA before the period of implantation (year $t + 1$), (ii) the proportion of females with placental scars before the period of implantation (year $t + 1$), and (iii) the proportion of females with fetuses after the period of implantation (year t). Ovulation rate (year t) was calculated as the proportion of females with CL before the period of implantation (year t).
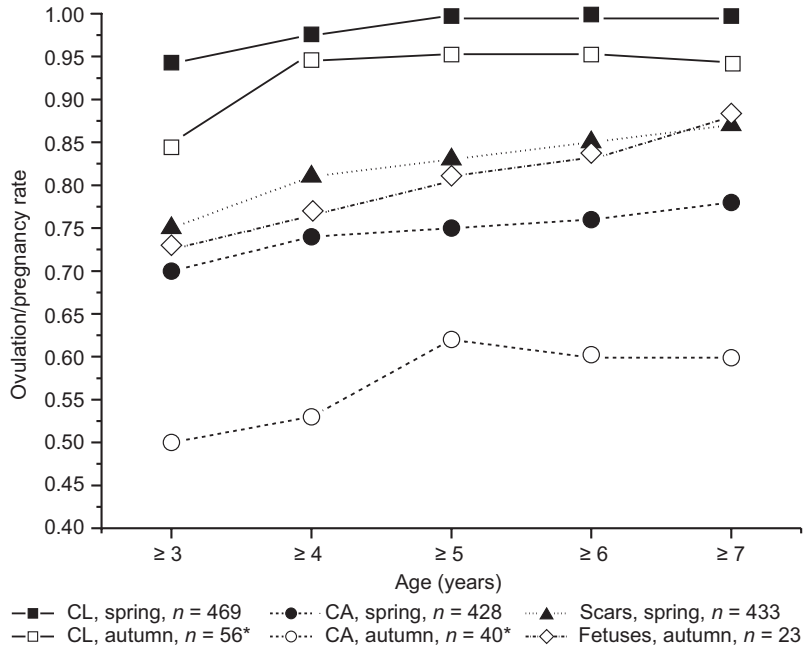
We compared pregnancy rates of females from the early and late 2000s because population growth ceased in the Finnish sea area in 2005 and the demographic structure of the population changed during the 2000s (Kauhala *et al.* 2012). We also calculated 'moving' pregnancy rates for 3-year periods (2000–2002, 2001–2003, 2002–2004, …, 2009–2011) because the population growth rate changed gradually (Kauhala *et al.* 2012) and annual sample sizes were too small in many years (Table 1). We used only samples from spring (pregnancy rate based on CA and scars) because the autumn sample (pregnancy rate based on fetuses) was too small to compare between time periods. The spring (pre-implantation) sample consisted of females hunted between 16 April and 29 June (85% from May) mainly (83%) from the Bothnian Bay and the Quark (ICES SD 31 and northern part of SD 30; Kauhala & Kunnasranta 2012), and only three adult females were by-caught in fishing gear. Therefore, there was very little spatial or temporal variation between years in the origin of the spring sample. We used Pearson's χ^2 test or Yates' corrected χ^2 test to compare the proportions of females with CL, CA, placental scars and fetuses in different samples.

Population numbers were estimated from annual aerial surveys during the peak moulting season in late May and early June (*see* Kauhala *et al.* 2012 for a detailed description of the method). Baltic grey seals usually breed in February–March on drift ice and exhibit some site fidelity for breeding and molting areas (Karlsson 2003, Karlsson *et al.* 2005). Because we used the spring sample, i.e. seals shot mainly from ice from the Finnish sea area, to compare pregnancy rates with population numbers, we also used population numbers from the Finnish sea area. However, because the entire Baltic grey seal population is considered a single population, we also compared the pregnancy rate of females in the Finnish sea area with that in the entire Baltic Sea population. It must be noted here that

Table 1. Pregnancy rate of 6–24-year-old Baltic grey seal females in different years based on females with *corpora albicantia* (CA) and those with placental scars before the period of implantation (spring sample). Pregnancy rate was calculated when the sample size (*n*) was at least ~30.

Year	CA	*n*	Pregnancy rate	Scars	*n*	Pregnancy rate
2000	7	9	–	2	2	–
2001	10	15	–	16	16	–
2002	25	29	0.86	29	30	0.97
2003	50	53	0.94	50	50	1.00
2004	52	56	0.93	57	57	1.00
2005	44	69	0.64	49	66	0.74
2006	3	3	–	2	3	–
2007	4	6	–	5	6	–
2008	31	43	0.72	34	45	0.76
2009	20	35	0.57	21	36	0.58
2010	13	17	–	18	21	–
2011	3	7	–	7	7	–
Total	263	343	0.77	291	340	0.86

Fig. 3. Ovulation and pregnancy rates of Baltic grey seal females starting from different ages and determined from the presence of *corpus luteum* (CL) and *corpus albicans* (CA) in spring and autumn, i.e., before and after the implantation period, placental scars in spring and fetuses in autumn. * Ovulation/pregnancy rates were determined from females killed after 1 July in order to get a larger data set.

Legend:
—■— CL, spring, *n* = 469   ···●··· CA, spring, *n* = 428   ···▲··· Scars, spring, *n* = 433
—□— CL, autumn, *n* = 56*   ···○··· CA, autumn, *n* = 40*   ···◇··· Fetuses, autumn, *n* = 23

Y axis: Ovulation/pregnancy rate
X axis: Age (years): ≥ 3, ≥ 4, ≥ 5, ≥ 6, ≥ 7

population size means the number of seals seen during aerial surveys and, e.g. weather conditions may affect the numbers. Seal numbers seen during aerial surveys should thus be treated as an index of population size. It is, however, a good estimate for the trend in population size (Harding *et al*. 2007), and there was no trend in the Finnish sea area after the mid-2000s (Fig. 1).

Results

Comparison between methods

Ovulation rate was significantly higher in the spring (pre-implantation) sample than in the autumn sample ($\chi^2 = 7.8$, df = 1, $p = 0.005$; Fig. 3), especially when the youngest age class was included. In autumn (including data from July), CL were larger in pregnant females (mean 16.7 mm ± SD 2.41, $n = 19$) than in non-pregnant females (14.1 mm ± 2.17, $n = 18$; *t*-test: $t = 3.4$, df = 34.9, $p = 0.002$). CL of females killed in spring averaged 14.4 mm ± 2.09 ($n = 347$). Furthermore, the pregnancy rate, determined on the basis of CA, was higher in the spring sample ($\chi^2 = 13.3$, df = 1, $p < 0.001$). CA were larger in spring (8.5 mm ± 1.64, $n = 251$) than in autumn

(7.1 mm ± 2.25, $n = 18$; *t*-test: $t = 2.6$, df = 18.3, $p = 0.019$). Because of significant differences between spring and autumn samples, with low numbers in the autumn dataset, we only used data from spring hereafter when comparing ovulation and pregnancy rates between age classes or time periods.

The pregnancy rate based on placental scars in spring tended to get higher values than that based on CA ($\chi^2 = 3.7$, df = 1, $p = 0.054$, $n = 406$ females with information of both CA and scars). However, the pregnancy rate derived from placental scars/CA in spring did not differ significantly from that derived from fetuses in autumn (scars: $\chi^2 = 0.12$, df = 1, $p = 0.725$; CA: $\chi^2 = 0.08$, df = 1, $p = 0.778$). In 94% of the females which had both CA and placental scars ($n = 263$) they were on the same side (right/left ovary and uterine horn). In 6% of the cases, CA and scars were either on opposite sides or there were signs of scars in both uterine horns. All of these females were ≥ 8 years old, and 82% were ≥ 10 years old.

In July, 4 out of 8 females determined as pregnant had only very small embryos, which were not measured. The head-body length of the fetus increased rapidly and linearly from late August onwards (Fig. 4).
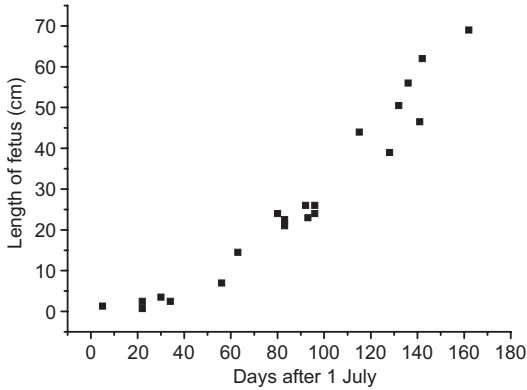
Fig. 4. The head-body length (from nose to flipper) of Baltic grey seal fetuses (*n* = 17), determined after 1 July in 2000–2012. From day 56 onwards: Length of fetus = 0.56 × days after 1 July − 25.1 (r^2 = 0.94, *F* = 206, df = 1, 14, *p* < 0.001).

Ovulation and pregnancy rates at different ages

The ovulation rate calculated using collective data was 0.94 (469 females that were > 2 years old), whereas that of ≥ 5-year-old females was 0.99 (*n* = 409; Figs. 3 and 5). The pregnancy rate of the 6–24-year-old females, i.e. females in the best reproductive age according to Bowen *et al.* (2006), was as high as 0.77–0.86,

depending on the method used, and the lowest in the 4–5-year-old females (0.54–0.56; Table 2). However, in our data the pregnancy rate of 7–11-year-old females was the highest: it was 0.86 according to both CA and scars. The proportion of females with CA/scars increased to the age of 9–10 years and gradually declined thereafter (Fig. 5). The oldest female with CA and placental scars in our data was a ~40-year old female. We found one case with uterine occlusion (in only one uterine horn): a 13-year-old female killed in 2009.

Pregnancy rate in different time periods

The pregnancy rate of all females (≥ 4 years old, determined from CA) differed between years (χ^2 = 28.4, df = 13, *p* = 0.008; Table 1). The pregnancy rate determined from CA or from placental scars was higher in 2000–2004 than in 2005–2011 (Table 3). However, among 4–5-year-old females, the pregnancy rate from CA did not differ significantly between the time periods (but sample sizes were small), although based on placental scars it tended to be lower during the latter period. Among 6–24-year-old females, the pregnancy rate derived from CA was as high as 0.89 in 2000–2004, but only 0.66
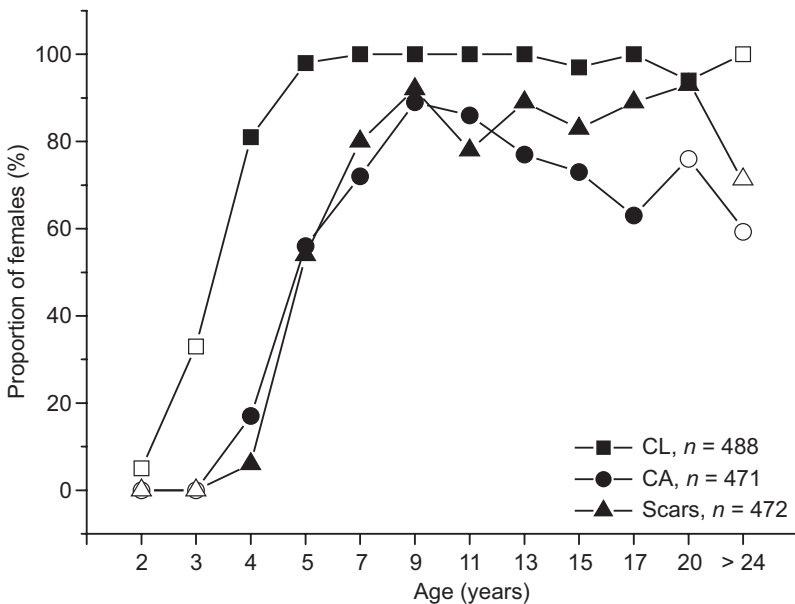

Fig. 5. The proportions of Baltic grey seal females of different ages with *corpora lutea* (CL), *corpora albicantia* (CA) and sings placental scars in the spring samples (the pre-implantation period) from 2000–2012. Two-year age groups were used for ≥ 5-year-old females to get larger data sets for each age group, i.e., age 5 = 5–6-year-old females, etc., except in older age classes where data for several age classes were pooled (17 = 17–19, 20 = 20–24). Points with sample sizes < 30 are marked with open symbols. Note that the pregnancy rate at age *t* = the proportion of females with CA/scars at age *t* + 1.

Table 2. Pregnancy rates of Baltic grey seal females of different age classes based on the number of females with *corpora albicantia* (CA) and those with placental scars in spring (before the implantation period), and the number of females with fetuses in autumn (after the implantation period) in 2000–2011. Pregnancy rate was calculated when the sample size (*n*) was at least 30.

Age (years)	CA	*n*	Pregnancy rate	Scars	*n*	Pregnancy rate	Fetus	*n*	Pregnancy rate
≥ 4	294	398	0.74	324	398	0.81	17	22	–
4–5	25	45	0.56	26	48	0.54	1	3	–
6–24	263	343	0.77	291	340	0.86	16	19	–
7–11	122	142	0.86	121	141	0.86	6	7	–
> 24	6	10	–	7	10	–	–	–	–

thereafter. The pregnancy rate of 6–24-year-old females differed, however, also between areas during the latter period (2005–2011). It was 0.62 (*n* = 141) in the Bothnian Bay and 0.81 (*n* = 39) in the other areas (χ^2 = 4.3, df = 1, *p* = 0.039). There was no difference between areas in 2000–2004. The decline in the pregnancy rate was thus sharper in the northernmost area, the Bothnian Bay, than in more southern areas.

The 'moving' pregnancy rate showed a declining trend (CA: *r* = –0.85, *p* = 0.002, scars: *r* = –0.94, *p* < 0.001; Fig. 6). The decreasing trend in pregnancy rate could be seen in both age groups (4–5-year-old and 6–24-year-old females), and the decline was sharper in the younger age group (but small sample size). The pregnancy rate of 6–24-year-old females correlated negatively with population size in the Finnish sea area (CA: *r* = –0.66, *p* = 0.039; scars: *r* = –0.84, *p* = 0.002) and with seal numbers in the whole Baltic Sea (CA: *r* = -0.78, *p* = 0.008; scars: *r* = –0.94, *p* < 0.001).

Discussion

Differences between the methods

Some differences between the results obtained with different methods existed. The pregnancy rate based on *corpus albicans* (CA) was higher according to the pre-implantation sample than according to the autumn sample, which points to the conclusion that some CA have indeed disappeared after the period of implantation as Boyd (1984a) reported. Therefore, only the samples of seal females killed before the implantation

period should be included when estimating pregnancy rate of the previous year from CA.

The pregnancy rate derived from placental scars (before implantation) tended to be higher (up to 99%) than that based on CA. In cases when CA and the placental scar were on opposite sides (usually they are on the same side, Atkinson 1997) or when there were signs of scars in both uterine horns, mainly concerned older females. In multiparous females, one can sometimes see signs of placental scars from earlier years (Ouellette & Ronald 1985), which may

Table 3. Pregnancy rates of Baltic grey seal females of different age classes for two time periods, 2000–2004 and 2005–2011, determined from the presence of *corpus albicans* (CA) and placental scars before the period of implantation (spring sample). Sample sizes are given in parentheses. Differences between the two time periods were tested with the χ^2-test, and the values for χ^2 and *p* are given (df = 1 for all tests). Sample sizes for 4–5-year-old females were small (< 30).

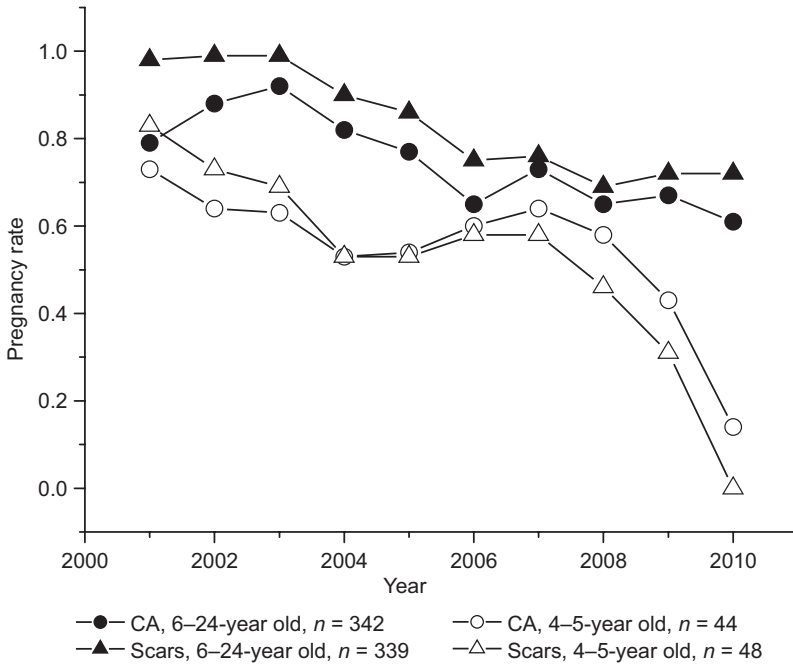| Period/Method	Age (years)	CA	Scars
2000–2004	≥ 4	0.86 (183)	0.96 (176)
2005–2011	≥ 4	0.64 (215)	0.70 (221)
	χ^2, *p*	24.3, < 0.001	32.6, < 0.001
2000–2004	4–5	0.63 (19)	0.70 (20)
2005–2011	4–5	0.48 (25)	0.25 (28)
	χ^2, *p*	0.74, 0.388	3.46, 0.063
2000–2004	6–24	0.89 (162)	0.99 (155)
2005–2011	6–24	0.66 (180)	0.74 (184)
	χ^2, *p*	25.9, < 0.001	44.3, < 0.001
2000–2004	7–11	0.94 (67)	1.00 (65)
2005–2011	7–11	0.78 (74)	0.74 (76)
	χ^2, *p*	7.3, 0.007	17.8, < 0.001

Fig. 6. Pregnancy rates of 4–5-year-old and 6–24-year-old females, determined from the presence of *corpus albicans* (CA) and placental scars in seal females killed before the period of implantation in spring in the Finnish sea area during different time periods (2000–2002, 2001–2003 … 2009–2011, i.e., the data were smoothed with three-year moving averages). Sample size for each point varied between 48 and 178 for 6–24-year old females. Sample sizes were small (5–16) for 4–5-year-old females.

result in overestimates of the pregnancy rate. However, pregnancy rate on the basis of placental scars/CA in spring and that based on fetuses in autumn did not differ significantly. Therefore, our estimates of pregnancy rates, based on several methods, should be fairly reliable. Also Boyd (1985) found that pregnancy rates derived from CA and fetuses were similar in grey seals.

Ovulation rate, especially that for younger age classes, was higher when calculated from the pre-implantation sample than from the autumn sample (Fig. 3), because CL may disappear after the implantation period if the female fails to become pregnant (Boyd 1984a). Ovulation rate should thus be calculated from the pre-implantation sample. Furthermore, if pregnancy rate is calculated from CL after implantation, the size of CL should be measured, and only large CLs (larger than about 16.5 mm) should be interpreted as indicators of pregnancy, because in non-pregnant females, CL are much smaller (if they persist) than those in pregnant females (Boyd 1984a). Using autumn CL (during pregnancy) may also lead to overestimation of the true birth rate due to fetal mortality: the pregnancy rate determined from fetuses was 0.875 and that from CL was 1.0 in the northwest Atlantic population (Hammill & Gosselin 1995).

Ovulation and pregnancy rates at different ages

Uterine occlusions, most probably caused by environmental pollutants, are a unique feature for Baltic seals, especially for the ringed seal (*Phoca hispida botnica*; e.g., Helle *et al.* 1976, Bergman 1999). Only one case with uterine occlusion was found in the present study, and no cases existed in Swedish grey seal data from the Gulf of Bothnia in 2002–2007 (Bäcklin *et al.* 2011). Reproductive health of Baltic grey seal females can therefore be considered normal today. Reproductive health of the ringed seal has also increased in recent years (Bäcklin *et al.* 2013a).

The ovulation rate was 0.33 in 3-year-old females (calculated from a small sample size), 0.81 in 4-year-old females and increased thereafter, being almost 1.0 after the age of five years. These results were in concordance with some earlier studies: the age of sexual maturity in grey seals is 3–5 years (Atkinson 1997), the ovulation rate of the 4-year-old females on the Herbides and Farne Islands was 0.80 (Boyd 1985) and the ovulation rate of grey seals aged five years and older approached 100%, e.g., on Sable Island, Canada (Bowen *et al.* 2006). The average age of

sexual maturity for grey seal females was four years in a low-density population of Iceland (Hauksson 2007). In the Atlantic stocks, the mean age at first parturition was 5.2–5.5 years but occasionally females gave birth at the age of three years (Hammill & Gosselin 1995, Schwarz & Stobo 2000).

In the present study, the pregnancy rate of all females ≥ 4-years-old was 0.74–0.81, which is close to the values given in earlier studies from the Baltic Sea (0.75–0.87; Harding *et al*. 2007, Bäckling *et al*. 2013a) and within limits given in Atlantic studies (0.66–0.94; Bowen *et al*. 2003, Harwood & Prime 1978). Boyd *et al*. (1999) estimated that pregnancy rates between 0.5 and 0.9 are normal for pinnipeds and they suggested that the pregnancy rate varies according to population density and food availability.

The lower pregnancy rate of the youngest females (4–5 years old) in the present study has also been shown in earlier studies (e.g., Boyd 1985, Schwarz & Stobo 2000, Bowen *et al*. 2006, Hauksson 2007, Bäcklin *et al*. 2013a). The pregnancy rate for adult females (6–24-year-old females: 0.77–0.86) in the present study for the whole study period was somewhat lower than the values given for some rapidly increasing populations: the pregnancy rate was as high as 0.955 during population increase in the Baltic Sea (Bäcklin *et al*. 2013a) and 0.88–0.97 in rapidly increasing Atlantic stocks (e.g. Boyd 1985, Hammill & Gosselin 1995, Hauksson 2007).

The pregnancy rate of grey seals decreases after the age of 24 years (Bowen *et al*. 2006, present study). Reproductive senescence is thus not evident in grey seals before the age of 25. However, even females over 40 years old can still be reproductively active (Bowen *et al*. 2006, present study). Probable reasons for senescence are reduced ovarian function, reduced transfer of nutrients to the fetus or reduced functionality of the placenta (Bowen *et al*. 2006). Producing offspring reduces the probability of survival and future reproductive success, i.e., there are costs of reproduction (e.g. Clutton-Brock *et al*. 1982, Stearns 1992). Old females thus tend to have lower pregnancy rates. The reproductive value of Baltic grey seals decreased after the age of five years (Kauhala *et al*. 2012).

Declining pregnancy rate during the 2000s

The pregnancy rate for 6–24-year-old females (from CA) was 0.89 during the early 2000s and declined thereafter being only 0.66 in the late 2000s. Our prediction of the decline in pregnancy rate at high population density was thus verified. Pregnancy rate from the early 2000s was close to values obtained in the rapidly increasing populations in the North Atlantic (e.g., Boyd 1985, Hammill & Gosselin 1995) and in the Baltic Sea (Bäcklin *et al*. 2013a), and it was similar in the Bothnian Bay and in the more southern areas. However, pregnancy rate in the latter time period, when population growth ceased in the Finnish sea area and also in Estonia (I. Jüssi pers. comm.), was lower, and it was lower in the Bothnian Bay than in the other Finnish sea areas. It was, however, within the limits of 'normal' pregnancy rate (Boyd *et al*. 1999). The decline in pregnancy rate, especially in the northernmost area, may point to the conclusion that grey seal numbers are close to the carrying capacity of the northern parts of the Baltic Sea.

The negative correlation between pregnancy rate and population size in the present study may thus be due to density-dependent processes acting on the population (e.g. Ricklefs 1973, Sinclair & Norton-Griffiths 1979, Begon *et al*. 1986, Flowerdew 1987). In long-lived K-strategist species, such as the grey seal, reduced fecundity is an important density-dependent factor acting on high densities (e.g., Clutton-Brock *et al*. 1982, Begon *et al*. 1986). Also, the survival rate of Baltic grey seal females, especially those < 10 years old, declined when population size increased (Kauhala *et al*. 2012). The fitness of an average individual is supposed to decline as a function of population density, and population size may thus affect reproductive parameters and also survival rates in seals (Hammill & Gosselin 1995, Bowen *et al*. 2006, Svensson *et al*. 2011). In Iceland, a high reproductive rate in a low-density grey seal population indeed suggests a density-dependent response to population numbers (Hauksson 2007).

Body condition may affect pregnancy rate, because it plays an important role in both implantation and maintenance of pregnancy in mam-

mals (Boyd 1984b, Bowen *et al*. 2006). Body condition (blubber thickness) of Baltic grey seals, especially in younger age classes, has indeed decreased during the 2000s (Bäcklin *et al*. 2013b). If population numbers are high in relation to food resources, individuals may have thinner fat reserves, which may, in turn, affect their pregnancy rate (e.g., Clutton-Brock *et al*. 1982, Atkinson 1997). In a rapidly increasing population, i.e., in a population which is below the environmental carrying capacity, females probably have larger fat reserves and reproduce at a younger age than in a high-density population (Atkinson 1997, Bowen *et al*. 2006, 2007, Svensson *et al*. 2011). In the present study, the pregnancy rate of the youngest females indeed declined more in the late 2000s than that of older females. Also, the survival rate of young seals is likely affected by their body condition and therefore may decrease when population density increases (Svensson *et al*. 2011). The increased mortality rate of young grey seal females found in the earlier study may, however, also be due to their increased proportion in the hunting catch and/or among by-caught seals (Kauhala & Kunnasranta 2012, Kauhala *et al*. 2012). The true number and demographic structure of by-caught seals in the Baltic Sea is unknown. It cannot, however, be ruled out that density-dependent factors also affect the population, especially in northern areas, and cause a higher mortality rate of young seals and a lower pregnancy rate of females.

Conclusions

Results of the present study point to the conclusion that density-dependent factors may affect the part of the Baltic grey seal population that mainly breeds and moults in the Finnish sea area. The population growth has ceased, pregnancy rate has declined and mortality rate of young females has increased in recent years. It is not, however, clear what is the carrying capacity of the Baltic Sea for grey seals today, and what are the resources (if any) regulating population size. There probably were even 100 000 Baltic grey seals in the early 20th century (e.g., Harding *et al*. 2007), but the carrying capacity may change over time (Svensson *et al*. 2011).

Other explanations, beside those based on density-dependent factors, to the decreased pregnancy rate during the latter half of the 2000s must also be considered. During mild winters when there is only little ice, many Baltic grey seal pups are born on land and their average body weights at weaning are lower than those born during colder winters on ice (Jüssi *et al*. 2008). Weather (ice) conditions in winter may thus affect the pregnancy rate of females later in life, because early growth and subsequent reproductive success are often linked in mammals, at least in males (Clutton-Brock *et al*. 1982). Climate and ice conditions probably also affected reproductive parameters of ringed seals (Chambellant *et al*. 2012). The impact of climate change on Baltic seal populations should be investigated.

The breeding success of males has not been taken into account in the present study. It is unknown whether the breeding success of males has changed, and how it might affect the pregnancy rate of females. The proportion of males in the population increased during the 2000s (Kauhala *et al*. 2012), which may have an effect on their reproductive success. Further research on this subject is needed.

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