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Demographic structure and mortality rate of a Baltic grey seal population at different stages of population change, judged on the basis of the hunting bag in Finland

Kaarina Kauhala[1], Markus P. Ahola[1] & Mervi Kunnasranta[2]

[1)] *Finnish Game and Fisheries Research Institute, Itäinen Pitkäkatu 3 A, FI-20520 Turku, Finland*
[2)] *University of Eastern Finland, Department of Biology, P.O. Box 111, FI-80101 Joensuu, Finland*

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We examined the demographic structure and mortality rate of the Baltic grey seal (*Halichoerus grypus*) population from the early 2000s when the population increased rapidly to the late 2000s when the growth rate slowed down. We calculated life tables based on the age structure of hunted grey seals in the Finnish sea area. The catch was treated as a sample of the dying part of the population. The catch was male biased and the proportions of female pups and mature males in the catch increased from the early to late 2000s. Annual mortality rate of the youngest age classes was high and higher among males than females, which resulted in low sex ratio (males to females) of the population. Sex ratio was, however, higher in the latter years due to the increased mortality rate of females, especially those < 10 years of age. Accordingly, the proportion of mature females in the population decreased and relatively fewer pups were produced during the late 2000s than in the early 2000s.

Introduction

The grey seal (*Halichoerus grypus*) is a top predator in the Baltic Sea ecosystem and its numbers have fluctuated during the past 100 years. The estimates of population size in the beginning of the 20th century vary from 80 000–100 000 (even 200 000) individuals (Harding & Härkönen 1999, Kokko *et al*. 1999). In the 1940s, high hunting pressure caused a sharp decline of the population to about 20 000 seals (e.g. Kokko *et al*. 1997, Harding & Härkönen 1999, Harding *et al*. 2007). Thereafter population decline continued due to environmental pollution by organochlorines, such as PCBs and DDT, and in the 1970s there probably were only 2000–3000 Baltic grey seals (Jensen *et al*. 1969, Almkvist 1978, Bergman & Olsson 1986, Kokko *et al*. 1997, Bergman 1999, Harding & Härkönen 1999). Most likely due to environmental toxins, Baltic grey and ringed seal (*Phoca hispida botnica*) females suffered from severe reproductive disturbances in the 1960s and 1970s (Bergman & Olsson 1986, Bergman 1999, Harding & Härkönen 1999, Nyman 2000, Bäcklin *et al*. 2003, Nyman *et al*. 2003, Bergman 2007) and productivity of the seal populations was low during several decades. Due to the decreased levels of organochlorines in the Baltic Sea during recent decades reproductive health of the seals improved, and today the pregnancy rate of grey seals is supposed to be normal (Bäcklin *et al*. 2010, 2011). Consequently, the population increased at an annual rate of 7.5%–8.5% since 1990 until recent years (Harding *et al*. 2007, Karlsson *et al*. 2007) and the population size is at present (2010) at least 23 000 individuals (Kunnasranta 2010).

The growing Baltic grey seal population has resulted in seal–fishery conflicts. Protection of the grey seal began in 1982 in Finland and in 1986 in Sweden, but due to the increased seal-induced damages to coastal fisheries, hunting of grey seals was resumed again in 1998 in Finland and in 2001 in Sweden. Grey seals are thus hunted in Finland mainly because they cause damage to coastal fisheries but sport and subsistence hunting for the skin, blubber and meat of the seals also takes place.

In Finland (including Åland), the annual hunting bag increased from 90 grey seals in 2000 to 617 individuals in 2009 (including 142 on Åland), and the annual hunting quota is today 1500 grey seals (including 450 in Åland; Suomen riistakeskus 2011, Ålands Landskapsregering 2011; Table 1). In Sweden, the annual quota is about 200 grey seals (Anon. 2007). The Swedish catch increased from 57 in 2001 to 126 in 2009 (Sälar och Fiske 2011). In addition to hunting, unknown number of grey seals dies as incidental by-catch of coastal fishery. Hunting affects mortality rates of individuals, and consequently, may alter age and sex structure, productivity and growth rate of seal populations (Kokko *et al*. 1997, Harding & Härkönen 1999, Kokko *et al*. 1999, Harding *et al*. 2007), if hunting mortality is additive to other sources of mortality, which is highly likely.

Here we examined the demographic structure and mortality rate of the Baltic grey seal population from 2000 to 2009 when the population increased but the growth rate gradually levelled off (Fig. 1). The study was based on the age structure of the hunting bag of grey seals in the Finnish sea area, while age structure of seals dying of other causes, such as by-catch, hunting in Sweden, illegal culling and natural causes, could not be taken into account because no systematic data exist or we had not access to these data. The hunting bag was treated as a sample of the dying part of the population.

We tested two hypotheses to be connected to the population growth rate: (1) the mortality rate of < 10-year-old females was lower in the early 2000s when the population increased at a higher rate than in the late 2000s, because the growth rate of the population is very sensitive to the mortality rate of females under 10 years of

Table 1. Annual catch of grey seals in different parts of the Finnish sea area and percentage of the total catch. 29 = SW archipelago (including Åland), 30 = Bothnian Sea, 31 = Bothnian Bay and 32 = Gulf of Finland.

Year	29		30		31		32		Total
	Number	Percentage	Number	Percentage	Number	Percentage	Number	Percentage	
2000	32	53	3	5	20	33	5	8	60
2001	56	39	51	35	32	22	5	3	144
2002	99	44	78	35	34	15	14	6	225
2003	95	30	106	34	86	27	28	9	315
2004	185	42	130	29	105	24	21	5	441
Subtotal	467	39.4	368	31.1	277	23.4	73	6.1	1185
2005	152	35	152	35	99	23	27	6	430
2006	144	55	61	23	19	7	36	14	260
2007	238	59	78	19	35	8	50	12	401
2008	291	50	150	26	100	17	46	8	587
2009	227	37	219	35	115	19	56	9	617
Subtotal	1052	45.8	660	28.8	368	16.0	215	9.4	2295
Total	1519	43.6	1028	29.6	645	18.5	288	8.3	3480

age (Harding *et al*. 2007); and (2) productivity of the population was higher in the early 2000s due to a higher proportion of females in reproductive age (> 4 years) in the population. Because pregnancy rate did not change much during the study period (Bäcklin *et al*. 2010) and the litter size is only one pup, higher productivity must be due to a higher proportion of reproducing females in the population. Also Lonergan *et al*. (2011) found that ceasing of the growth rate of a grey seal population was not due to reductions of fecundity. Since the study was based on the age structure of hunted grey seals, we discuss the possible effect of hunting on the mortality rate and demography of the grey seal population, and consequent changes in pup production and population size. We also discuss the possible need to adjust the hunting pressure according to the present demographic structure of the population to prevent population decline.

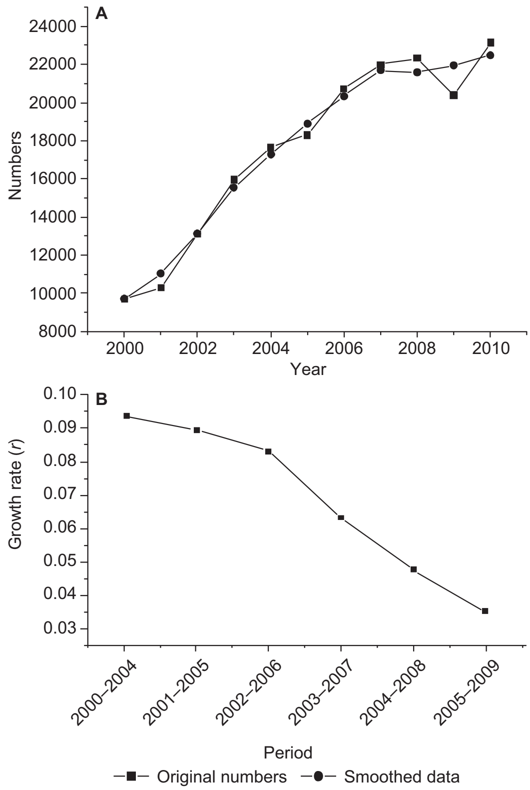

Fig. 1. (**A**) Numbers of grey seals seen during seal monitoring counts (aerial surveys) in May/June in the Baltic Sea (Kunnasranta 2010), and (**B**) the estimated growth rate (r) for each of the 5-year periods ($r = \ln[N_{t+1}/N_t]$).

Material and methods

The hunting season for the grey seal in Finland lasts from 16 April to 31 December (16 April–31 January on the island of Åland). Samples from hunted seals were collected from hunters between 2000 and 2009 from the Finnish sea area (including Åland): Bothnian Bay (ICES subdivision area 31), Bothnian Sea (ICES SD 30), SW archipelago (ICES SD 29) and the Gulf of Finland (ICES SD 32; Fig. 2). We received samples of 1068 grey seals (43% males and 57% females). Most samples (77%) were from spring (16 April–30 June), especially from the molting season of seals when they lie on land (from May to early June), and a majority of these were females from the Bothnian Bay (Fig. 2). The 'autumn' samples were from 1 July to 31 December/31 January, i.e. seals hunted after the molting period.

Samples accounted 31% of the total catch (n = 3480; Suomen riistakeskus 2011, Ålands landskapsregering 2011) from the Finnish sea area. Fourty-nine percent of the samples came from the Bothnian Bay, although only 19% of the grey-seal catch was from the area (Table 1 and Fig. 3). The corresponding figures for the SW archipelago were 14% and 44%. Because our samples were biased, we calculated correction coefficients (% catch/% samples) for the samples from each sea area and period (below) to weigh the samples from each area correctly, i.e. so that they would better reflect the true catch.

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

The population growth rate (r) was obtained from annual aerial surveys during the peak moulting season in late May and early June, i.e. from the total numbers of counted grey seals in the entire Baltic Sea area. Standard aerial surveys have been used in Sweden from 2000 (Karlsson *et al*. 2007) and in Finland

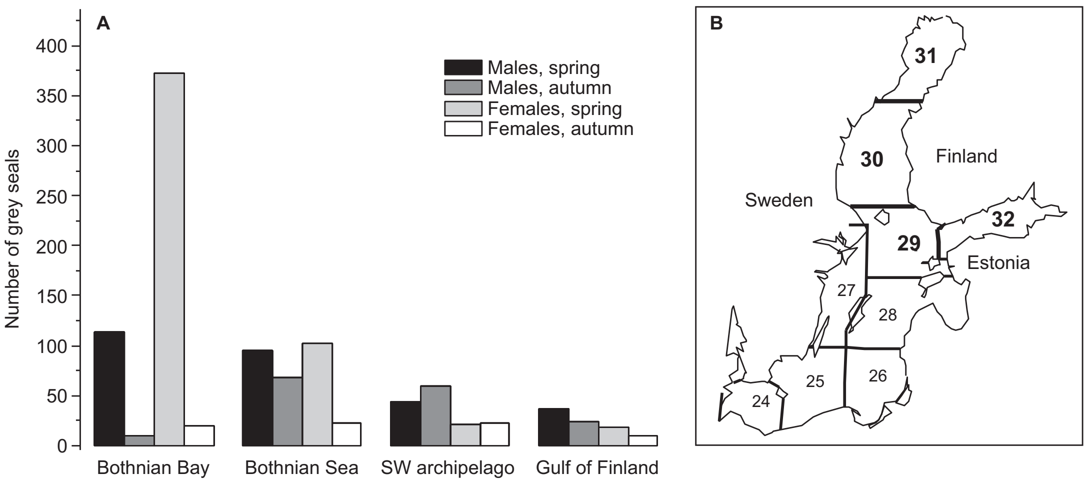

Fig. 2. (**A**) Samples of hunted grey seals from spring and autumn in 2000–2009, received from hunters from the different parts of the Finnish sea area. (**B**) ICES subdivision areas: 29 = SW archipelago, 30 = Bothnian Sea, 31 = Bothnian Bay and 32 = Gulf of Finland. Source map: http://www.helcom.fi/environment2/biodiv/fish/en_GB/ICES_subdivisions/.

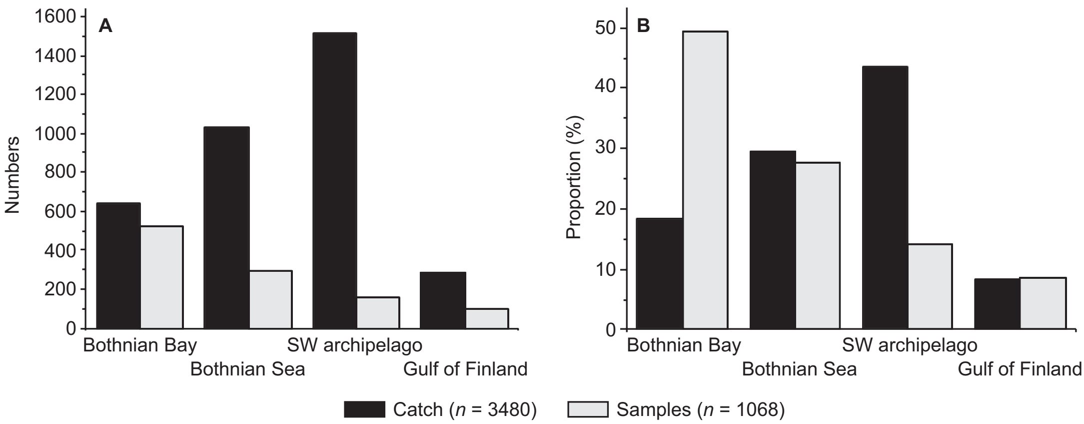

Fig. 3. (**A**) Numbers and (**B**) proportions of the grey seal catch and samples of seals received from hunters in different parts of the Finnish sea area in 2000–2009.

from 2005. Original numbers of counted seals were smoothed using three-year moving average (Fig. 1), because hazardous events (e.g. weather conditions and seal migrations during the two week annual monitoring periods) may influence the estimated population size. Population growth rate (r) was determined as $\ln[N_{t+1}/N_t]$, where N_{t+1} is the population size in year $t + 1$ and N_t the population size in year t. The growth rate was calculated for each period (below).

We calculated ‘moving life tables’ for 5-year periods starting from 2000–2004, then removing the first year and adding one year after the last, i.e. 2001–2005, 2002–2006, 2003–2007, 2004–2008, and ending in 2005–2009. We thus combined the data for each 5-year period to calculate life tables because of fairly small numbers of samples from hunted seals each year (i.e. to get larger data). Although five years is a short period for life-table calculations (and determining the population growth rate) for seals with a long generation time and life-span (Harding *et al*. 2007), at least the changes in mortality rates of the youngest age classes will most probably be revealed by these tables. Since the population growth rate slowed down (Fig. 1), these 'moving' life tables would thus show the gradual change in survival and mortality rates of seals.

We calculated the life tables from the Finnish hunting bag treated as a sample of the dying part of the population, assuming that the mortality rate of different age classes differ (i.e. individuals that die during a certain time do not represent a random sample of the population). We also assumed that the capture is a sample of the animals that died in the course of one year, starting from the age of 0.3 years (the mean age of hunted pups). We transformed the numbers of dying animals to frequencies of deaths and multiplied them by a correction factor e^{rx} (where r = growth rate and x = age) to obtain the probability of dying (Caughley 1977). We then calculated the survival values: the sum of the probabilities of dying must equal the probability of surviving in the age class 0.3, because all individuals finally die. The probabilities of surviving in the other age classes were obtained by subtraction. We then transformed the survival values to frequencies (= age structure of the population, S_x) by multiplying them by the correction factor e^{-rx}. Then we added the number of pups born in late winter (age class 0) using the pregnancy rates given below. To obtain the final survival values (l_x), we divided the S_x values by the frequency of the zero-age class and multiplied them by the correction factor e^{rx}. We then calculated the probability of dying ($d_x = l_x - l_{x+1}$), and the annual mortality rate of each age class ($q_x = d_x/l_x$). Life expectancy (e_x) was calculated with the formula:

$$T_x/l_x, \text{ where } T_x = \sum[(l_x + l_{x+1})/2]. \qquad (1)$$

The productivity of the population was based on the Finnish and Swedish data (Bäcklin *et al.* 2010, Bäcklin, *in litt.*). A pregnancy rate of 0.845 for 4–20-year-old females (95.5% for 6–20-year-old females and 65% for 4–5-year-old females) was used for all periods, since this value was presented for 2002–2009 (Bäcklin *et al.* 2010, Bäcklin, *in litt.*). These values are fairly similar to those given by Boyd (1985) for grey seals of Farne Islands and Herbides. Productivity of the population was expressed as the number of pups produced by a population of 1000 seals (both sexes and all age classes included) in late winter. Reproductive value (RV_x) of females in each age class was calculated with the formula:

$$RV_x = m_x + \sum_{t=x+1}^{t=\infty} \frac{m_t l_t}{l_x}, \qquad (2)$$

where m_x is the birth rate of the individual in age-class x, m_t is the birth rate of the individual in age-class t and l_t/l_x is the probability that the individual will survive from age x to age t.

To calculate the demographic structure of the whole population, we combined the S_x columns of the female and male life tables assuming a sex ratio 1:1 at birth (Hewer 1964).

Differences between the age structures and sex ratios of the catches were tested using a χ^2-test. The level of significance was set to 0.05.

Results

Recent changes in population numbers and growth rate

In 2000 in the Baltic Sea, the minimum seal population size (i.e. molting seals seen during seal monitoring in late May–early June) was about 10 000. More than 20 000 grey seals were seen during the monitoring counts in 2009 and about 23 000 in 2010 (Fig. 1A; Kunnasranta 2010). The population growth rate declined gradually from 0.094 in 2000–2004 to 0.035 in 2005–2009 (Fig. 1B). The number of seals counted in the Finnish sea area increased from 3000 in 2000 to 8200 in 2009 and 9600 in 2010 (Kunnasranta 2010).

Demographic structure of the Finnish hunting bag of grey seals

There were more males (57%) than females (43%) in the total catch in 2000–2009 ($\chi^2 = 8.9$, df = 1, $p = 0.003$). The proportions of males in the catches were 53% and 59% in 2000–2004 and 2005–2009, respectively. The sex ratio of the catch was the lowest in the Bothnian Bay and the highest in the SW archipelago ($\chi^2 = 69.7$, df = 1, $p < 0.001$; Table 2).

The proportions of pups (individuals < one year) and mature (4–20 years) individuals varied

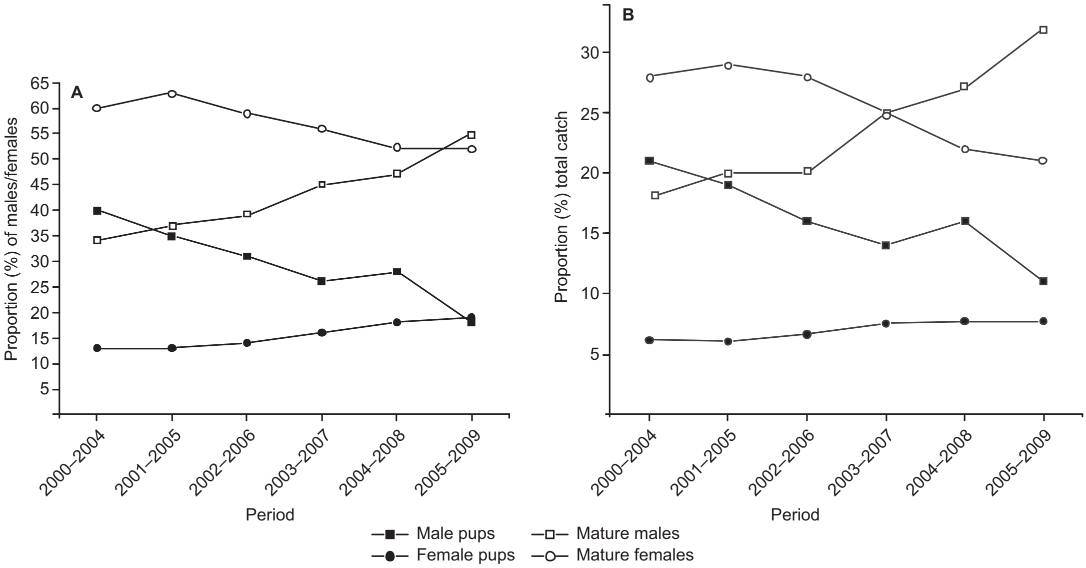

Fig. 4. Proportions of pups and mature individuals (4–20-year old) among (**A**) males and females, and (**B**) among all hunted Baltic grey seals during different periods.

between sea areas and periods (Table 2 and Fig. 4). The proportion of pups was the lowest in the Bothnian Bay in 2000–2004 and the highest in the Gulf of Finland in 2005–2009 ($\chi^2 = 15.3$, df = 1, $p < 0.001$), whereas the proportion of mature females was high in the Bothnian Bay and low in the Gulf of Finland and in the SW archipelago. The proportion of mature males was especially high in the SW archipelago and in the Bothnian Sea in 2005–2009.

The age structure of the total catch differed also between sexes. During the first period, the proportion of pups was higher among males (40%) than among females (13%; $\chi^2 = 38.8$, df = 1, $p < 0.001$), whereas the proportion of mature seals (4–20-year-old) was higher among females (60%) than among males (34%; $\chi^2 = 30.0$, df = 1, $p < 0.001$; Fig. 4A). The proportion of pups decreased among males (difference between the first and last period: $\chi^2 = 31.7$, df

Table 2. Percentage of pups, 1–3-year-old, mature (4–20-year-old) and > 20-year-old seals in the samples of grey seals collected from hunters from the Finnish sea areas during the first and last periods. M = male, F = female. 29 = SW archipelago, 30 = Bothnian Sea, 31 = Bothnian Bay and 32 = Gulf of Finland.

Period/area		29		30		31		32	
		M	F	M	F	M	F	M	F
2000–2004	Pups	27.9	7.3	25.4	7.7	2.7	1.1	25.0	10.0
	1–3-yr-old	16.2	14.7	16.6	8.9	5.4	7.5	10.0	15.0
	Mature	20.6	11.8	14.8	26.0	15.0	64.0	30.0	5.0
	> 20-yr-old	1.5	0.0	0.6	0.0	0.0	4.3	0.0	5.0
	Total	66.2	33.8	57.4	42.6	23.1	76.9	65.0	35.0
2005–2009	Pups	9.1	6.8	12.1	8.1	5.0	5.0	26.7	16.0
	1–3-yr-old	23.9	12.5	5.6	5.6	6.5	11.2	17.3	6.6
	Mature	38.6	9.1	38.0	26.6	12.5	55.0	20.0	8.0
	> 20-yr-old	0.0	0.0	0.8	3.2	0.3	4.5	2.7	2.7
	Total	71.6	28.4	56.5	43.5	24.3	75.7	66.7	33.3

= 1, $p < 0.001$) and was almost equal in males and females during the last period (18% and 19%, respectively). Contrary, the proportion of mature females in the total catch decreased (χ^2 = 6.1, df = 1, $p = 0.013$) and that of mature males increased (χ^2 = 26.6, df = 1, $p < 0.001$) during the study period, and the total catch in 2005–2009 consisted of 32% and 22% of mature males and mature females, respectively (Fig. 4B). The proportion of pups in the total catch was 27% in 2000–2004 and 19% in 2005–2009.

Life tables of grey seal populations

Survival rates of females especially under the age of 10 years decreased during the study period and correlated negatively with population size (survival to the age of 1 year: $r = -0.98$, $p = 0.001$, $n = 6$; to 5 years: $r = -0.98$, $p = 0.001$; to 10 years: $r = -0.96$, $p = 0.002$), whereas the survival rate of males increased with increasing population sizes (to 1 year: $r = 0.96$, $p = 0.003$; to 5 years: $r = 0.97$, $p = 0.001$; to 10 years: $r = 0.95$, $p = 0.004$; Appendixes 1–6, Fig. 5). During the first period (2000–2004), 76% of females and 38% of males were still alive at the age of one year, and 64% of females and 25% of males were alive at the age of 5 years (i.e. reached the age when most individuals reproduce; Fig. 5 and Appendix 1). Fifty-three percent of females and 88% of males died before the age of 10 years. During the last period (2005–2009), differences between the sexes were small: only 55% of females survived to the age of one year and 40% to the age of 5 years, the corresponding figures for males being 53% and 37%; and 73% of females and 82% of males died before the age of 10 years. Due to the change in the survival rate of females under the age of 10 years, the sex ratio (males/females) of the entire population (in summer) increased from 0.41 in 2000–2004 to 0.84 in 2005–2009, and the ratio of mature animals (4–20-year-old) from 0.31 to 0.79 (Figs. 6 and 7).

According to all life tables (Appendixes 1–6), the sex ratio declined towards the older age classes but the decline was slower during the later periods (Fig. 6). Accordingly, the proportion of reproducing females (5–20-year-old) declined during the study period from 38% in 2000–2004 to 31% in 2005–2009 (calculated for a population in winter before the pups are born). Supposing a pregnancy rate of 0.845, a population of 1000 seals in late winter produced 317 pups in 2000–2004 but only 259 pups in 2005–2009 (Fig. 7). Reproductive value (in 2005–2009) was the highest for 5–9-year-old females and they produced 57% of pups (Fig. 8).

The life expectancy of the new-born female pups declined during the study period from 10.4 years in 2000–2004 to 6.6 years in 2005–2009 (Appendixes 1–6). During the earlier periods,

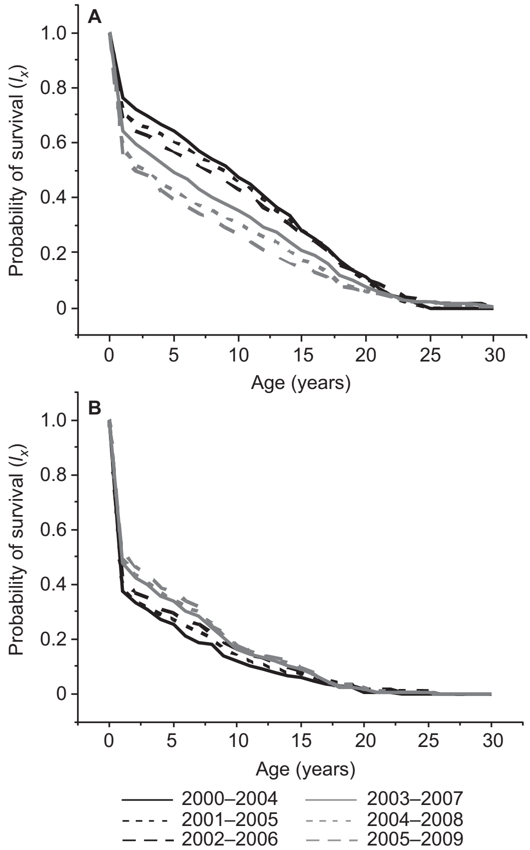

Fig. 5. Probability of (**A**) female and (**B**) male Baltic grey seals of being alive at different ages during different periods. The differences in the survival rates (l_x) between the first and last periods was tested with a χ^2-test. Females, age 1 year: χ^2 = 55.2, df = 1, $p <$ 0.001; age 5 years: χ^2 = 78.8, df = 1, $p < 0.001$; age 10 years: χ^2 = 63.1, df = 1, $p < 0.001$. Males, age 1 year: χ^2 = 39.6, df = 1, $p < 0.001$; age 5 years: χ^2 = 29.4, df = 1, $p < 0.001$; age 10 years: χ^2 = 10.7, df = 1, $p = 0.001$.

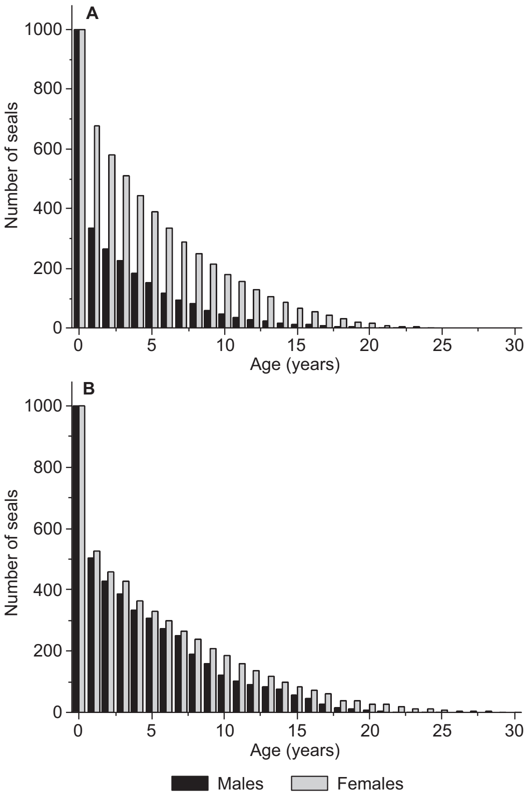

Fig. 6. Age structures of the Baltic grey seal populations by sex, estimated on the basis of the life tables calculated assuming that the age structure of the Finnish hunting bag illustrates the age structure of the dying part of the population in (**A**) 2000–2004 and (**B**) 2005–2009. Age structures were calculated for populations with 1000 newborn males and females.

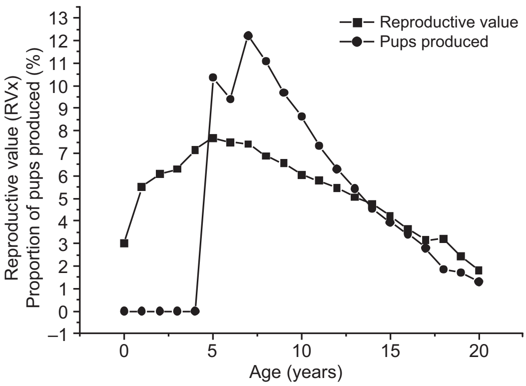

Fig. 8. Reproductive value of females (RV_x) and the proportion of pups produced by females of different ages in 2005–2009.

life expectancy of females was the highest (about 12 years) at the age of 0.3 years. During

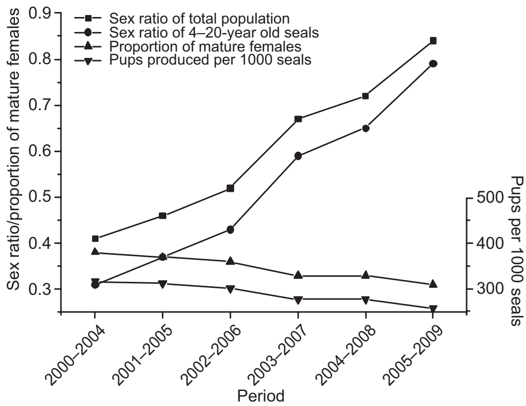

Fig. 7. Sex ratio of the entire population and that of mature seals, proportion of mature females in the population and pups produced by 1000 seals in winter.

the later periods, however, life expectancy was the highest (9.5 years) at the age of 1–2 years. Life expectancy of males was lower. It was the highest (7.3–8.3 years) at the age of 1–2 years, and the maximum value did not change much during the study period. The life expectancy of male pups increased, however, during the study period from 4.0 to 5.5 years.

Discussion

Reliability of methods

In the life table calculations, three variables were incorporated into the formulas: population growth rate, age structure of the hunting bag and pregnancy rate. Thus these variables — and only these variables — affect the results of the life table calculations. If they were estimated correctly, then the life tables should give reliable results. The sex ratio of the catch does not affect the life tables because they were calculated separately for males and females.

During the study period, the estimated population growth rate decreased from 0.094 to 0.035 (i.e. from 9.8% to 3.6%). According to monitoring counts in Sweden during 2000–2004 (Karlsson *et al*. 2007), the numbers of grey seals increased with an annual rate of about 8.5%, and the theoretical maximum annual growth rate of a grey seal population is 10%–13% (Bowen *et al*. 2003, Harding *et al*. 2007). Our values for the earlier years thus agree well with the estimates given in other studies. The numbers of grey seals seen during annual monitoring counts have not increased during recent years in the Finnish sea area (Kunnasranta 2010), and have only slightly increased in Sweden (T. Härkönen pers. comm.), which points to the conclusion that the population growth is ceasing. Our values for the population growth rate should thus be fairly reliable.

The catch was treated as a sample of the dying individuals, not as a random sample of the population, because it is likely that the mortality rate differs between age classes. If the age structure of the catch is similar to that of individuals dying of other causes, our life tables should give a reliable picture of the survival and mortality rates of different age classes. If, however, many seals die of other causes and their age structure differs much from that of hunted seals, then our life tables may be biased. Unfortunately, little data on the age structure of seals caught as by-catch or stranded are available. According to a fairly small data ($n = 48$ females and 78 males) from Sweden from 2002–2007 (Bäcklin *et al.* 2011), 77% of females caught as by-catch were < 11 years old, which is a higher value than the proportion of females < 11 years in the Finnish hunting bag (72% for 2003–2007). If the number of females caught as by-catch is high, then the true mortality rate of females (< 10–11 years) may be even greater than the values given in our life tables. Young seals seem to be the most vulnerable to incidental catch in fishing gear. In the Swedish data, 19% of males caught as by-catch were < 1 year old, the corresponding figure in the present study being 18%. During a study on the Norwegian coast, even 25% of tagged grey seal pups were caught as by-catch in fishing gear (Bjørge *et al.* 2002). In Sweden, 62% of seals caught as by-catch were males (Bäcklin *et al.* 2011). It is thus possible that the proportion of pups (especially males) is slightly underestimated in the catch when individuals caught as by-catch are not taken into account. More data on the age structure and amount of seals caught as by-catch and seals that died of other causes are needed.

The pregnancy rate was estimated from the Finnish and Swedish data (Bäcklin *et al.* 2010, Bäcklin, *in litt.*). The values are close to those estimated in other studies of grey seals (e.g. Boyd 1985, Wiig 1991, according to Harding *et al.* 2007) and should thus be reliable.

Changes in the demographic structure of hunted seals

During recent years, a larger proportion of grey seals were hunted in the SW archipelago and in the Gulf of Finland than during the early 2000s (Table 1), whereas a smaller proportion of seals were hunted in the Bothnian Bay. One reason for the decreased proportion of catch in the Bothnian Bay was probably poor ice conditions, because in the area, seals are mainly hunted in late spring on ice. As a result of campaigns to hunt seals that cause most problems to coastal fishery in the SW archipelago, the proportion of catch from the area has increased.

The sex ratio of the catch increased during the study period, because the catch in the SW archipelago contained more males (69%), whereas the catch in the Bothnian Bay contained more females (76%), most of which were mature individuals (Fig. 2 and Table 2). Accordingly, the proportion of mature females in the total catch decreased whereas that of mature males increased during the study period (Fig. 4). However, the proportion of female pups in the total catch increased from 6.1% in 2000–2004 to 7.7% in 2005–2009, since there were more female pups in the catch in the SW archipelago (7%) and also in the Gulf of Finland (13%) than in the Bothnian Bay (3.6%).

The reasons for the female-biased catch in the Bothnian Bay and the male-biased catch in the SW archipelago are most probably the timing of hunting and the behavioural differences between the sexes. There may be differences in the timing of molting between seals of different ages and between sexes. For example in harbor seals (*Phoca vitulina*) yearlings molt first, subadults second, adult females third and adult males last (Daniel *et al.* 2003). Therefore, it is possible that mature females molt earlier on ice than males and are therefore more likely to become potential targets to hunters in the Bothnian Bay, where seals are mainly hunted in late spring on ice. Pups molted already before the hunting season and their proportion in the catch was low. Adult males may start molting later mainly on land. It is likely that in autumn males are shot more often than mature females when hunting takes place near the coast, as probably happens in the SW archipelago and in the Bothnian Sea, where especially males move and are hunted around fishing gear to reduce the problems caused by seals to coastal fishery. The reduced proportion of male pups in the catch (Fig. 4 and Table 2) in the SW archipelago, and thus also in the total catch, may partly result from the increased proportion of adult males in the catch.

Changes in the mortality rate and productivity of the population

The mortality rate of females < 10 years of age increased during the study period. Our first hypothesis was thus supported by the results. The life tables showed that the increased mortality rate of females < 10 years of age resulted in a decreased proportion of mature females in the population. Hence, the relative pup production of the population decreased during the study period. The estimated numbers of pups produced in relation to the population size (317 in 2000–2004 and 259 in 2005–2009 per a population of 1000 seals) are close to the values given in the literature (population size = 3.5 × the number of pups; e.g. Harwood & Prime 1978). According to the formula, a population of 1000 seals will produce 286 pups. The pup production during the earlier period was thus a little higher and that during the latter period a little lower than the value given for British grey seals (Bonner 1976, Harwood & Prime 1978).

Our second hypothesis that productivity of the population was higher in the early 2000s than during the later years due to the higher proportion of females at reproductive age was thus also supported by the results. Females aged 5–9 years have a high reproductive value and are therefore very important for the population, as was also shown by Harding *et al*. (2007).

The change in the survival rate of females < 10 years of age affects the reproductive rate of the population and finally the population growth rate. The grey seal is a typical K-strategist with a long life-span and low productivity and even small changes in the mortality rate of females may therefore have a great impact on the population growth rate (Harwood & Prime 1978). Also Harding *et al*. (2007) found that the population growth rate was very sensitive to a decrease in the survival rate of females, especially those < 10 years of age.

Human-induced mortality

At present, the annual hunting quotas for the Baltic grey seal are 1500 in Finland (including Åland) and more than 200 in Sweden (Sälar och Fiske 2011), i.e. about 7% of the minimum population estimate of ca. 24 000 seals in 2011 and about 5.6% of the entire population (assuming that 80% of seals are seen during monitoring). Less than 50% of the quota had, however, been used annually (Suomen riistakeskus 2011, Sälar och Fiske 2011, Ålands Landskapsregering 2011), thus the hunting pressure in the whole Baltic Sea was about 3.5% of the minimum population estimate. In Finland alone, on average 566 grey seals were hunted per year in 2008–2010, when the number of counted seals in the Finnish sea area was about 9000, i.e. the annual hunting pressure was 6.2% of the minimum population size and about 5% of the total population.

According to Harding *et al*. (2007), hunting a constant proportion of a population is more harmful than taking a constant number of seals each year. The quasi-extinction risk increases sharply at low mean growth rates, and if density-dependent factors impact population numbers. Therefore, if the population growth is ceasing, a constant hunting pressure of 5%–7%, enabled by the hunting quotas for the whole Baltic Sea, would increase the risk of population decline. In Finland, the true hunting pressure has been 5%–6% during recent years when population growth has ceased (Kunnasranta 2010). Because of moulting-site fidelity of grey seals and because many seals are hunted close to the moulting season, it is sensible to compare the number of hunted seals in Finland to the number of counted seals in the Finnish sea area to prevent over-exploitation of the local population

(Karlsson 2003, Karlsson *et al*. 2005).

A greater problem than the size of the total hunting bag may be the high mortality rate of young females which in a few years results in a low proportion of mature females in the population. With the present age and sex structure and a low growth rate of the population, the population produces relatively fewer pups than earlier. To prevent population decline, hunting should be focused even more on males and less on females and should, therefore, be done more often in the vicinity of fishing gear, because individuals visiting them are usually males (Lehtonen & Suuronen 2010). Also seal population management would benefit, if hunting targets the animals which commonly feed near fishing gear. This strategy of hunting would partly mitigate the conflict between seals and fishery (Graham *et al*. 2011).

Besides hunting, many seals are incidentally caught in fishery. Globally, the by-catch mortality likely has significant demographic effects on many populations of marine mammals (e.g. Read *et al*. 2005). The total number of Baltic grey seals caught as by-catch is unknown but an estimate of 300 seals per year is given for Estonia alone (M. Vetemaa, pers. comm.), and in some years the number may be as high as 1000 seals in the whole Baltic Sea (Lunneryd & Westerberg 1997, Harding *et al*. 2007). It is thus possible that the number of seals that die as by-catch even exceed the number of hunted seals, and drowning in fishing gear may be an important mortality factor of Baltic grey seals. If these seals were added to the hunting bag, the total human-induced mortality would be much higher. Better knowledge of the numbers and age structure of seals caught as by-catch would enable us to more reliably estimate the effect of human-induced mortality on the population structure, mortality rate and productivity.

According to Wade (1998), potential biological removal (PBR) is the maximum number of animals (excluding natural mortalities) that may be removed from a marine-mammal population while allowing the stock to reach or maintain its optimum sustainable population. According to Wade (1998) PBR for the Baltic grey seal is the product of the minimum population size (24 000), one-half of the maximum productivity rate (1/2 of 13% = 0.065) and the optimistic recovery factor, which for this stock could be 1.0 (the value for stocks of unknown status, but known to be increasing). PBR calculated using that formula would be 1560 for Baltic grey seals, which is just slightly greater than the annual hunting quota for Finnish grey seals. Although only 50% of the quota is used annually, the pooled number of seals hunted in Finland and Sweden together with unknown numbers of seals caught as by-catch may be close to PBR in the Baltic Sea. Therefore, the volume of human-induced seal removal should be taken into account when planning management and conservation measures for the Baltic grey seal population.

Other sources of mortality

The survival rate of pups during their first year of life (0.53 for males and 0.55 for females) in 2005–2009 was a little lower as compared with the value (0.62 for females) given for British grey seals by Hall *et al*. (2001), and 0.70 given for Baltic grey seals without density dependence (Svensson *et al*. 2011), whereas the survival rate of female pups in 2000–2004 (0.76) was higher than that of British seals. Survival rates of the adults in our study (0.87–0.92 in 4–15-year-old individuals) fall into the range found earlier for the Baltic grey seal (Harding *et al*. 2007, Svensson *et al*. 2011), and for other seal populations (e.g. Harwood & Prime 1978, Smith 1987, Wickens & York 1997, Schwartz & Stobo 2000).

According to the life tables, the mortality rate of young pups during their first months of life (< 0.3 years) both before and after weaning was high in Finland. As stated above, young pups after weaning are often caught incidentally in coastal fishery (Bjørge *et al*. 2002). Other factors, which may affect mortality rates of pups include climate change (Jüssi *et al*. 2008). Many small pups may die during winters when ice cover is week, because at the time of weaning grey-seal pups born on land in the Baltic Sea (where seals often give birth on ice) are smaller than those born on ice, and pup survival is related to their weight (Hall *et al*. 2001, Jüssi *et al*. 2008). There were some very mild winters in the 2000s, when ice cover was almost absent in the main breeding areas of grey seals in Finland, which may have resulted in low survival rates of pups before weaning. This is an important subject for further research because the mortality rate of young pups is independent of hunting mortality (hunting season begins in mid-April when the pups are about two months old) but is partly due to unpredictable events (such as weather), and may have a great influence on the population structure of grey seals. According to Harding *et al*. (2007), the risk for extinction increases as the occurrence of unpredictable events increases. We must, however, keep in mind that juvenile survival rates are also dependent on population density: they may decrease rapidly with increasing density (Svensson *et al*. 2011). Because the growth rate of the Baltic grey seal population seems to be ceasing and there are changes in the age structure, pup production and survival rates of the population (e.g. the survival rate of female pups decreased with increasing population numbers), we cannot rule out the possibility that the population is approaching the carrying capacity of the environment. However, the survival rate of male pups increased with increasing population numbers, which points to the conclusion that the increased mortality rate of females is not density-dependent. Because poor ice conditions or other hazardous events should also affect pups of both sexes, the increased mortality rate of young females is likely a result of increased human-induced mortality.

Conclusions

The present age structure and low growth rate of the population is a result of an increased mortality rate of females, especially those < 10 years of age. Consequently, the proportion of mature females decreased in the population, resulting in a relatively lower pup production during the late 2000s than in the earlier periods. To prevent a population decline, hunting should be targeted more at males, and thus should take place more often in the vicinity of fishing gear. Further research should be done to reveal true numbers and the demographic structure of seals caugth as by-catch, and also the effects of unpredictable events (such as weather conditions) on seal populations.

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Appendix 1. Life tables of female and male grey seals constructed on the basis of hunted grey seals (N = 443) in 2000–2004 in Finland. A correction factor (e^{rx}) was used when the frequencies of each age class in the catch/population were altered to probabilities of dying/surviving, because population was increasing (r = 0.094). Accordingly, when the probabilities of surviving were altered to the age structure of the population, a correction factor (e^{-rx}) was used. A pregnancy rate of 0.85 for females (4–20 years; Bäcklin 2011) was used to calculate the zero age class. S_x = age structure of the population, l_x = probability of being alive at age x, d_x = probability of dying at age x, q_x = annual mortality rate of age class x, e_x = life expectancy at age x.

Age (x)	Females					Age (x)	Males				
	S_x	l_x	d_x	q_x	e_x		S_x	l_x	d_x	q_x	e_x
0	1000	1.000	0.192	0.192	10.39	0	1000	1.000	0.487	0.487	3.962
0.30		0.808	0.045	0.056	11.74	0.30		0.513	0.136	0.265	6.244
1	675	0.763	0.043	0.057	11.41	1	334	0.377	0.048	0.126	7.312
2	580	0.719	0.023	0.032	11.07	2	266	0.330	0.021	0.065	7.295
3	511	0.696	0.032	0.046	10.42	3	226	0.308	0.034	0.109	6.766
4	444	0.664	0.025	0.037	9.89	4	184	0.275	0.024	0.087	6.531
5	389	0.640	0.033	0.051	9.26	5	153	0.251	0.039	0.156	6.105
6	336	0.607	0.037	0.062	8.73	6	117	0.212	0.023	0.107	6.140
7	287	0.569	0.028	0.050	8.27	7	95	0.189	0.008	0.041	5.814
8	248	0.541	0.027	0.050	7.68	8	83	0.182	0.044	0.241	5.038
9	215	0.514	0.042	0.081	7.06	9	58	0.138	0.015	0.107	5.482
10	180	0.472	0.020	0.043	6.64	10	47	0.123	0.022	0.178	5.080
11	157	0.452	0.045	0.100	5.91	11	35	0.101	0.009	0.088	5.070
12	128	0.407	0.040	0.097	5.51	12	29	0.092	0.011	0.121	4.511
13	106	0.367	0.034	0.093	5.05	13	23	0.081	0.016	0.197	4.065
14	87	0.333	0.050	0.150	4.52	14	17	0.065	0.006	0.093	3.940
15	67	0.283	0.032	0.113	4.23	15	14	0.059	0.008	0.138	3.294
16	54	0.251	0.035	0.140	3.71	16	11	0.051	0.017	0.330	2.742
17	43	0.216	0.043	0.201	3.23	17	7	0.034	0.006	0.171	2.847
18	31	0.172	0.037	0.217	2.92	18	5	0.028	0.004	0.156	2.330
19	22	0.135	0.025	0.182	2.59	19	4	0.024	0.015	0.610	1.669
20	16	0.110	0.039	0.355	2.05	20	1	0.009	0.000	0.000	2.500
21	10	0.071	0.023	0.321	1.90	21	1	0.009	0.000	0.000	1.500
22	6	0.048	0.015	0.303	1.56	22	1	0.009	0.009	1.000	0.500
23	4	0.034	0.016	0.477	1.02						
24	2	0.018	0.018	1.000	0.50						

Appendix 2. Life tables of female and male grey seals constructed on the basis of hunted grey seals (N = 555) in 2001–2005 in Finland. A correction factor (e^{rx}) was used when the frequencies of each age class in the catch/population were altered to probabilities of dying/surviving, because population was increasing (r = 0.090). Accordingly, when the probabilities of surviving were altered to the age structure of the population, a correction factor (e^{-rx}) was used. A pregnancy rate of 0.85 for females (4–20 years; Bäcklin 2011) was used to calculate the zero age class. S_x = age structure of the population, l_x = probability of being alive at age x, d_x = probability of dying at age x, q_x = annual mortality rate of age class x, e_x = life expectancy at age x.

Age (x)	Females					Age (x)	Males				
	S_x	l_x	d_x	q_x	e_x		S_x	l_x	d_x	q_x	e_x
0	1000	1.000	0.250	0.250	9.905	0	1000	1.000	0.499	0.499	4.342
0.3		0.750	0.041	0.055	12.037	0.3		0.501	0.113	0.226	7.178
1	631	0.709	0.037	0.052	11.704	1	345	0.388	0.051	0.131	8.124
2	547	0.672	0.018	0.027	11.320	2	275	0.337	0.017	0.051	8.271
3	487	0.654	0.024	0.036	10.622	3	238	0.320	0.029	0.091	7.693
4	429	0.630	0.027	0.043	10.004	4	198	0.291	0.018	0.061	7.409
5	375	0.603	0.024	0.040	9.432	5	170	0.273	0.026	0.096	6.861
6	329	0.579	0.030	0.052	8.802	6	140	0.247	0.019	0.077	6.536
7	286	0.549	0.024	0.044	8.254	7	119	0.228	0.026	0.112	6.041
8	250	0.525	0.031	0.059	7.609	8	96	0.202	0.038	0.187	5.742
9	215	0.494	0.035	0.070	7.057	9	72	0.165	0.022	0.134	5.944
10	183	0.459	0.026	0.056	6.553	10	57	0.142	0.022	0.152	5.790
11	158	0.433	0.041	0.094	5.913	11	44	0.121	0.014	0.115	5.739
12	131	0.393	0.039	0.100	5.476	12	36	0.107	0.013	0.124	5.419
13	107	0.353	0.032	0.092	5.029	13	28	0.094	0.015	0.164	5.112
14	89	0.321	0.042	0.130	4.485	14	22	0.078	0.004	0.047	5.015
15	71	0.279	0.028	0.101	4.079	15	19	0.075	0.011	0.150	4.239
16	58	0.251	0.039	0.156	3.482	16	15	0.063	0.014	0.227	3.898
17	45	0.212	0.050	0.238	3.032	17	10	0.049	0.011	0.224	3.897
18	31	0.162	0.028	0.175	2.823	18	7	0.038	0.003	0.070	3.877
19	24	0.133	0.038	0.285	2.316	19	6	0.035	0.016	0.441	3.129
20	15	0.095	0.026	0.275	2.040	20	3	0.020	0.000	0.000	4.200
21	10	0.069	0.026	0.380	1.624	21	3	0.020	0.000	0.000	3.200
22	6	0.043	0.018	0.429	1.312	22	3	0.020	0.009	0.433	2.200
23	3	0.024	0.014	0.578	0.922	23	1	0.011	0.000	0.000	2.500
24	1	0.010	0.010	1.000	0.500	24	1	0.011	0.000	0.000	1.500
						25	1	0.011	0.011	1.000	0.500

Appendix 3. Life tables of female and male grey seals constructed on the basis of hunted grey seals (N = 685) in 2002–2006 in Finland. A correction factor (e^{rx}) was used when the frequencies of each age class in the catch/population were altered to probabilities of dying/surviving, because population was increasing (r = 0.083). Accordingly, when the probabilities of surviving were altered to the age structure of the population, a correction factor (e^{-rx}) was used. A pregnancy rate of 0.85 for females (4–20 years; Bäcklin 2011) was used to calculate the zero age class. S_x = age structure of the population, l_x = probability of being alive at age x, d_x = probability of dying at age x, q_x = annual mortality rate of age class x, e_x = life expectancy at age x.

Age (x)	Females					Age (x)	Males				
	S_x	l_x	d_x	q_x	e_x		S_x	l_x	d_x	q_x	e_x
0	1000	1.000	0.268	0.268	9.549	0	1000	1.000	0.471	0.471	4.685
0.3		0.732	0.046	0.063	11.902	0.3		0.529	0.104	0.197	7.420
1	615	0.685	0.044	0.064	11.696	1	381	0.425	0.053	0.125	8.122
2	529	0.641	0.018	0.028	11.496	2	307	0.371	0.020	0.054	8.215
3	474	0.623	0.030	0.048	10.838	3	267	0.351	0.040	0.113	7.657
4	415	0.593	0.026	0.044	10.378	4	218	0.312	0.017	0.055	7.565
5	365	0.567	0.024	0.043	9.843	5	189	0.294	0.024	0.081	6.980
6	321	0.543	0.030	0.055	9.263	6	160	0.270	0.018	0.066	6.552
7	279	0.513	0.026	0.051	8.771	7	138	0.253	0.029	0.114	5.980
8	244	0.487	0.026	0.054	8.217	8	112	0.224	0.039	0.175	5.682
9	212	0.461	0.028	0.061	7.656	9	85	0.185	0.021	0.116	5.781
10	183	0.432	0.025	0.058	7.122	10	69	0.163	0.018	0.112	5.476
11	159	0.407	0.041	0.102	6.534	11	57	0.145	0.015	0.104	5.105
12	131	0.366	0.028	0.076	6.216	12	47	0.130	0.014	0.110	4.641
13	112	0.338	0.035	0.103	5.684	13	38	0.116	0.020	0.174	4.153
14	92	0.303	0.036	0.120	5.277	14	29	0.095	0.011	0.115	3.923
15	75	0.267	0.025	0.095	4.929	15	24	0.084	0.017	0.204	3.367
16	62	0.242	0.034	0.140	4.393	16	17	0.067	0.028	0.410	3.101
17	49	0.208	0.050	0.242	4.026	17	9	0.040	0.009	0.237	3.908
18	34	0.157	0.019	0.123	4.154	18	7	0.030	0.002	0.054	3.966
19	28	0.138	0.031	0.228	3.669	19	6	0.029	0.012	0.431	3.165
20	20	0.107	0.019	0.180	3.603	20	3	0.016	0.000	0.000	4.186
21	15	0.087	0.023	0.262	3.284	21	3	0.016	0.000	0.000	3.186
22	10	0.065	0.023	0.355	3.272	22	3	0.016	0.007	0.438	2.186
23	6	0.042	0.011	0.260	3.798	23	1	0.009	0.000	0.000	2.500
24	4	0.031	0.003	0.096	3.958	24	1	0.009	0.000	0.000	1.500
25	3	0.028	0.010	0.344	3.323	25	1	0.009	0.009	1.000	0.500
26	2	0.018	0.000	0.000	3.806						
27	2	0.018	0.000	0.000	2.806						
28	2	0.018	0.004	0.225	1.806						
29	1	0.014	0.004	0.315	1.185						
30	1	0.010	0.010	1.000	0.500						

Appendix 4. Life tables of female and male grey seals constructed on the basis of hunted grey seals (N = 722) in 2003–2007 in Finland. A correction factor (e^{rx}) was used when the frequencies of each age class in the catch/population were altered to probabilities of dying/surviving, because population was increasing (r = 0.063). Accordingly, when the probabilities of surviving were altered to the age structure of the population, a correction factor (e^{-rx}) was used. A pregnancy rate of 0.85 for females (4–20 years; Bäcklin 2011) was used to calculate the zero age class. S_x = age structure of the population, l_x = probability of being alive at age x, d_x = probability of dying at age x, q_x = annual mortality rate of age class x, e_x = life expectancy at age x.

Age (x)	Females					Age (x)	Males				
	S_x	l_x	d_x	q_x	e_x		S_x	l_x	d_x	q_x	e_x
0	1000	1.000	0.288	0.288	8.211	0	1000	1.000	0.391	0.391	5.322
0.3		0.712	0.069	0.097	10.348	0.3		0.609	0.110	0.181	7.426
1	593	0.644	0.052	0.080	10.427	1	459	0.498	0.062	0.125	7.959
2	512	0.592	0.027	0.046	10.316	2	377	0.436	0.027	0.061	8.022
3	458	0.565	0.039	0.068	9.813	3	332	0.410	0.043	0.104	7.510
4	401	0.526	0.034	0.064	9.511	4	280	0.367	0.019	0.052	7.323
5	352	0.492	0.026	0.052	9.133	5	249	0.348	0.029	0.082	6.696
6	313	0.467	0.037	0.080	8.610	6	214	0.319	0.020	0.063	6.251
7	271	0.429	0.025	0.059	8.311	7	189	0.299	0.039	0.131	5.640
8	239	0.404	0.025	0.062	7.801	8	154	0.260	0.048	0.183	5.417
9	210	0.379	0.025	0.065	7.287	9	118	0.212	0.034	0.161	5.519
10	185	0.354	0.026	0.074	6.762	10	93	0.178	0.020	0.112	5.480
11	160	0.328	0.034	0.104	6.260	11	77	0.158	0.015	0.093	5.111
12	135	0.294	0.022	0.073	5.928	12	66	0.143	0.012	0.081	4.585
13	117	0.272	0.032	0.117	5.358	13	57	0.132	0.018	0.140	3.945
14	97	0.241	0.033	0.135	5.001	14	46	0.113	0.021	0.181	3.507
15	79	0.208	0.018	0.088	4.706	15	35	0.093	0.023	0.244	3.171
16	68	0.190	0.031	0.161	4.110	16	25	0.070	0.024	0.340	3.035
17	53	0.159	0.043	0.272	3.802	17	15	0.046	0.011	0.244	3.341
18	36	0.116	0.015	0.131	4.035	18	11	0.035	0.001	0.035	3.261
19	30	0.101	0.025	0.247	3.568	19	10	0.034	0.008	0.246	2.362
20	21	0.076	0.017	0.219	3.577	20	7	0.025	0.015	0.597	1.968
21	15	0.059	0.016	0.278	3.442	21	3	0.010	0.000	0.000	3.142
22	10	0.043	0.015	0.349	3.575	22	3	0.010	0.005	0.453	2.142
23	6	0.028	0.006	0.219	4.223	23	1	0.006	0.000	0.000	2.500
24	5	0.022	0.000	0.000	4.265	24	1	0.006	0.000	0.000	1.500
25	4	0.022	0.007	0.317	3.265	25	1	0.006	0.006	1.000	0.500
26	3	0.015	0.000	0.000	3.551						
27	3	0.015	0.000	0.000	2.551						
28	2	0.015	0.006	0.375	1.551						
29	1	0.009	0.003	0.319	1.181						
30	1	0.006	0.006	1.000	0.500						

Appendix 5. Life tables of female and male grey seals constructed on the basis of hunted grey seals (N = 653) in 2004–2008 in Finland. A correction factor (e^{rx}) was used when the frequencies of each age class in the catch/population were altered to probabilities of dying/surviving, because population was increasing (r = 0.048). Accordingly, when the probabilities of surviving were altered to the age structure of the population, a correction factor (e^{-rx}) was used. A pregnancy rate of 0.85 for females (4–20 years; Bäcklin 2011) was used to calculate the zero age class. S_x = age structure of the population, l_x = probability of being alive at age x, d_x = probability of dying at age x, q_x = annual mortality rate of age class x, e_x = life expectancy at age x.

Age (x)	Females					Age (x)	Males				
	S_x	l_x	d_x	q_x	e_x		S_x	l_x	d_x	q_x	e_x
0	1000	1.000	0.334	0.334	7.226	0	1000	1.000	0.399	0.399	5.106
0.3		0.666	0.082	0.123	9.626	0.3		0.601	0.126	0.210	7.166
1	549	0.584	0.068	0.117	9.930	1	447	0.475	0.050	0.106	7.933
2	462	0.516	0.020	0.038	10.195	2	381	0.425	0.026	0.060	7.815
3	424	0.496	0.044	0.089	9.599	3	341	0.399	0.044	0.110	7.283
4	368	0.452	0.026	0.057	9.498	4	289	0.355	0.017	0.049	7.125
5	331	0.426	0.030	0.070	9.044	5	262	0.338	0.036	0.106	6.464
6	294	0.397	0.024	0.061	8.684	6	224	0.302	0.018	0.058	6.169
7	263	0.372	0.020	0.053	8.213	7	201	0.285	0.041	0.146	5.518
8	237	0.353	0.024	0.067	7.647	8	164	0.243	0.039	0.162	5.375
9	211	0.329	0.022	0.067	7.160	9	131	0.204	0.038	0.187	5.314
10	188	0.307	0.027	0.087	6.636	10	101	0.166	0.019	0.115	5.423
11	163	0.280	0.025	0.088	6.224	11	86	0.147	0.016	0.106	5.060
12	142	0.255	0.015	0.058	5.778	12	73	0.131	0.008	0.063	4.603
13	128	0.241	0.034	0.142	5.101	13	65	0.123	0.016	0.134	3.879
14	104	0.206	0.031	0.148	4.864	14	54	0.106	0.018	0.165	3.401
15	85	0.176	0.016	0.093	4.623	15	43	0.089	0.019	0.211	2.973
16	73	0.160	0.029	0.183	4.045	16	32	0.070	0.021	0.302	2.633
17	57	0.130	0.045	0.342	3.841	17	21	0.049	0.023	0.469	2.557
18	36	0.086	0.008	0.089	4.578	18	11	0.026	0.001	0.036	3.371
19	31	0.078	0.017	0.219	3.977	19	10	0.025	0.005	0.183	2.479
20	23	0.061	0.008	0.138	3.953	20	8	0.020	0.011	0.561	1.922
21	19	0.053	0.010	0.191	3.506	21	3	0.009	0.004	0.440	2.738
22	15	0.043	0.016	0.386	3.214	22	2	0.005	0.000	0.000	3.500
23	9	0.026	0.003	0.124	3.917	23	2	0.005	0.000	0.000	2.500
24	7	0.023	0.000	0.000	3.400	24	2	0.005	0.000	0.000	1.500
25	7	0.023	0.012	0.530	2.400	25	2	0.005	0.005	1.000	0.500
26	3	0.011	0.000	0.000	3.538						
27	3	0.011	0.000	0.000	2.538						
28	3	0.011	0.004	0.381	1.538						
29	2	0.007	0.002	0.323	1.177						
30	1	0.005	0.005	1.000	0.500						

Appendix 6. Life tables of female and male grey seals constructed on the basis of hunted grey seals (N = 625) in 2005–2009 in Finland. A correction factor (e^{rx}) was used when the frequencies of each age class in the catch/population were altered to probabilities of dying/surviving, because population was increasing (r = 0.035). Accordingly, when the probabilities of surviving were altered to the age structure of the population, a correction factor (e^{-rx}) was used. A pregnancy rate of 0.85 for females (4–20 years; Bäcklin 2011) was used to calculate the zero age class. S_x = age structure of the population, l_x = probability of being alive at age x, d_x = probability of dying at age x, q_x = annual mortality rate of age class x, e_x = life expectancy at age x.

Age (x)	Females					Age (x)	Males				
	S_x	l_x	d_x	q_x	e_x		S_x	l_x	d_x	q_x	e_x
0	1000	1.000	0.355	0.355	6.633	0	1000	1.000	0.384	0.384	5.477
0.3		0.645	0.093	0.145	9.033	0.3		0.616	0.091	0.148	7.585
1	526	0.552	0.053	0.096	9.493	1	502	0.525	0.061	0.116	7.814
2	459	0.498	0.019	0.038	9.467	2	428	0.464	0.030	0.064	7.769
3	426	0.479	0.054	0.113	8.836	3	387	0.434	0.045	0.103	7.266
4	365	0.425	0.030	0.070	8.912	4	335	0.390	0.023	0.058	7.044
5	328	0.395	0.024	0.061	8.545	5	305	0.367	0.027	0.073	6.447
6	298	0.371	0.029	0.079	8.065	6	273	0.340	0.020	0.057	5.913
7	265	0.342	0.021	0.061	7.710	7	249	0.321	0.070	0.219	5.243
8	240	0.321	0.030	0.094	7.179	8	188	0.251	0.032	0.128	5.574
9	210	0.291	0.023	0.077	6.868	9	158	0.218	0.042	0.192	5.319
10	187	0.269	0.032	0.120	6.402	10	123	0.176	0.023	0.129	5.467
11	159	0.237	0.026	0.111	6.206	11	104	0.154	0.012	0.076	5.201
12	137	0.210	0.023	0.107	5.922	12	92	0.142	0.008	0.058	4.590
13	118	0.188	0.025	0.133	5.573	13	84	0.134	0.011	0.082	3.844
14	99	0.163	0.017	0.103	5.353	14	75	0.123	0.024	0.197	3.142
15	85	0.146	0.014	0.099	4.911	15	58	0.099	0.022	0.220	2.790
16	74	0.131	0.020	0.153	4.397	16	44	0.077	0.025	0.326	2.435
17	61	0.111	0.035	0.313	4.098	17	28	0.052	0.023	0.451	2.371
18	40	0.077	0.003	0.042	4.736	18	15	0.028	0.004	0.153	2.906
19	37	0.073	0.015	0.212	3.923	19	12	0.024	0.006	0.238	2.340
20	28	0.058	0.006	0.100	3.841	20	9	0.018	0.011	0.587	1.916
21	25	0.052	0.013	0.241	3.214	21	4	0.008	0.003	0.393	2.927
22	18	0.039	0.015	0.368	3.077	22	2	0.005	0.000	0.000	3.500
23	11	0.025	0.003	0.103	3.577	23	2	0.005	0.000	0.000	2.500
24	10	0.022	0.000	0.000	2.931	24	2	0.005	0.000	0.000	1.500
25	9	0.022	0.014	0.645	1.931	25	2	0.005	0.005	1.000	0.500
26	3	0.008	0.000	0.000	3.528						
27	3	0.008	0.000	0.000	2.528						
28	3	0.008	0.003	0.386	1.528						
29	2	0.005	0.002	0.326	1.174						
30	1	0.003	0.003	1.000	0.500						