

Estimates of the size of the Baltic grey seal population based on photo-identification data

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ABSTRACT

The size of the year 2000 summer population of grey seals in the Baltic Sea was estimated using identification of individual seals from photographs taken over a period of 6 years. Photos were taken at haul-out sites within all major grey seal areas in the semi-closed Baltic Sea. The point estimate is 15,631, based on a value for annual survival of identification markings of 0.904, which was also estimated using the photo-id data, with 95% confidence limits from 9,592 to 19,005. The estimate is subject to an unknown, but probably small, upward bias resulting from the risk of failure to identify all individuals in the photographs used for the analysis. An estimated minimum of 15,950 seals were counted at moulting haul-outs in 2003, which thus provides a lower bound on the population size in that year and represents 80% of the photo-id point estimate.

Hiby, L., Lundberg, T., Karlsson, O., Watkins, J., Jüssi, M., Jüssi, I. and Helander, B. 2007. Estimates of the size of the Baltic grey seal population based on photo-identification data. *NAMMCO Sci. Publ.* 6: 163-175.

INTRODUCTION

Grey seals (*Halichoerus grypus*) were once numerous in the Baltic Sea. A mere 100 years ago the population was estimated, based on hunting statistics, to comprise approximately 88,000 to 100,000 animals (Harding and Härkönen 1999). In the late 1970s the population was reduced to less than 4,000 individuals due to intense hunting and a disease complex caused by environmental contaminants, mainly PCBs and DDTs (Bergman and Olsson 1985, Bergman 1999). During recent decades the situation has improved and annual counts during moult indicate a growth rate of approximately 7.5% a year (Karlsson and Helander 2005) for the Swedish part of the population.

The current monitoring strategy was developed during the 1970s when the situation for Baltic grey seals was critical and management was directed to saving the few seals that

remained. The main focus of monitoring at the time was towards the detection of population trends while the actual size of the population was of lesser interest. With a growing grey seal population and a management strategy that includes culling as a way to mitigate seals/fisheries conflicts, there is an increased need to estimate the size of the population.

A photo-identification (photo-id) survey was initiated in 1994, with the aim of studying grey seal movements (Karlsson *et al.* 2005). This photo-id project was expanded to derive an accurate estimate of grey seal population size in the Baltic, based on mark-recapture techniques. Seals were photographed during the summer at all major haul-out sites in Swedish waters from 1995 to 2000 (Fig. 1). The survey was extended to Estonia in 1998 and Finland in 2000 so that almost all major haul-out sites in the Baltic were

Fig. 1. Grey seals haul out in large numbers to moult in May and early June in the Baltic Sea. (Photo: Torkel Lundberg)



visited during the final year of the study. Photo-id uses re-sightings of animals with distinctive markings as a method for studying population size and movement patterns as well as other population parameters. The technique is non-invasive and relatively inexpensive, compared to traditional tagging methods, and has been used successfully on several whale, dolphin and seal species (e.g. Biggs 1982, Clapham and Mayo 1990, Würsig and Würsig 1997). In this paper we use the results of the photo-id survey to estimate the size of the Baltic grey seal population.

METHODS

Study Area

Figure 2 shows the location of summer haul-outs selected for photography of individual seals. To accommodate the effects of variation in sampling intensity, data from the haul-outs were grouped into 7 geographical areas: A to G. The division into areas was based on proximity of the haul-outs on the assumption that seal movement between nearby haul-outs would be sufficient to negate the effects of any residual variation in sampling intensity.

Data collection

Each major haul-out was visited by boat 2 to 3 times each summer (June - September) with at least 2 weeks between successive trips to avoid temporal autocorrelation in the data. Data from grey seal haul-outs in the North Sea (Hiby 1994) show that the re-sighting frequency levels out after approximately 10 to 14 days. Most photographs were obtained in June, July and August, i.e. well after the breeding season and completion of moult.

All photographs were taken from the shore using a 35-mm (Canon EOS-1) still camera with an 840 mm auto focus lens and monochrome film (Ilford XP-2 or Kodak T-max). Each haul-out was approached slowly using an inflatable boat, causing the seals to move into the water but avoiding excessive disturbance to prevent seals from being chased away. The average group size was 67 seals. The photographer was dropped off on the islands while an assistant acted as a decoy by driving the boat along the shore (on the left or the right side of the photographer). This kept the seals interested and hence close to shore allowing the photographer to obtain (left and right) profile views of the head and neck area.

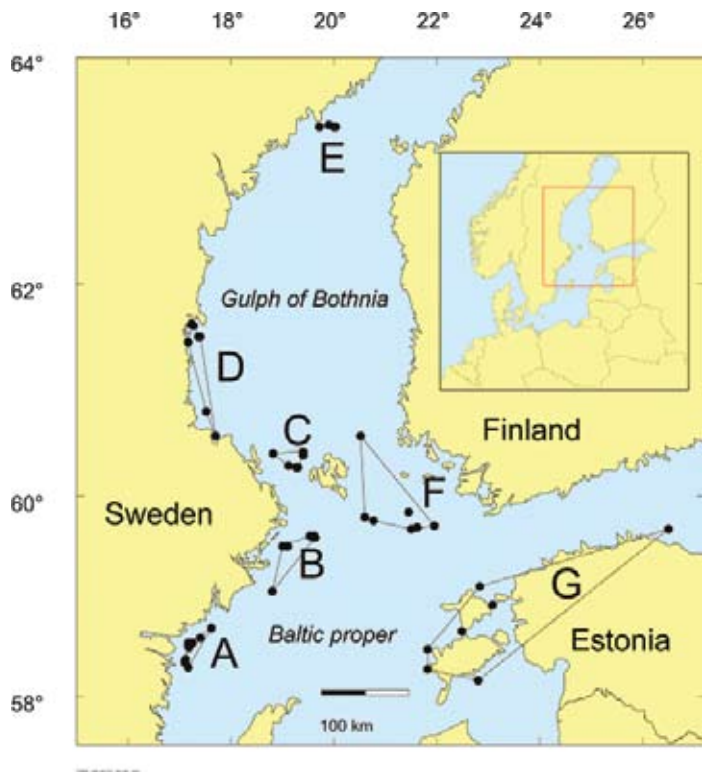


Fig. 2. Study area in the Baltic Sea, with sites grouped into subareas for analyses.

Profile photographs were taken of all “well-marked” seals in the group. Well-marked seals, mostly adult females, have a distinct black and white pelage pattern that could be recognized from a subsequent photograph. Frame numbers showing opposite sides of the same seal were noted. During data analysis left and right profiles were treated separately but any seal in the catalogue that was known from both sides provided a release for both analyses (left and right), even if only 1 side was photographed on any subsequent occasion.

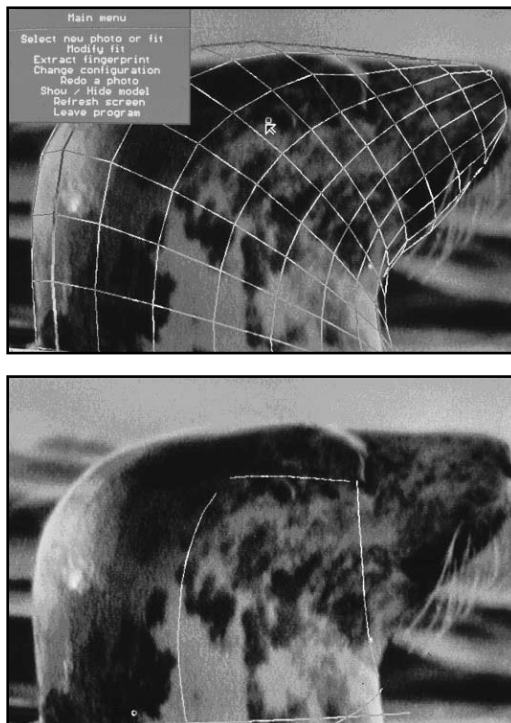
Image processing

Each set of frames exposed during a visit by the photographer to a single haul-out constitutes a “session”. The frames within each session were inspected to identify the number of individuals photographed from left and right sides and 1 or more acceptable frames of each individual scanned into a desktop computer. The resulting digital images were then processed to extract a sample of the pelage pattern on the side of the seal’s head to act as a “fingerprint”, uniquely identifying the seal when seen from that side.

The sample area, or “cell”, is a roughly rectangular region extending from the ear to the eye and down to the average position of the waterline (Fig. 3). Acceptable frames were those taken at no more than 65° from square-on to the cell in which at least 50% of the cell area was visible.

Purpose-written image-processing software was used to extract the samples via a 3-D surface model of the head and neck to compensate for differences in viewpoint and posture (Hiby and Lovell 1990). This allowed similarity scores between samples extracted from photographs of the same side to be calculated even when the camera angles and postures were different. All pairs of samples were compared using a program that allowed for error in positioning of the sample region of up to 50% of the width of the region. Those pairs of photographs that generated a correlation above a pre-set threshold were then inspected by eye to confirm that they represented a likely match. The final inspection stage ensured that the risk of falsely matching photographs was negligible.

Fig. 3. The 3D surface model has been orientated, scaled and shaped so that the positions of the model nose, ear and eye coincide, as closely as possible, with those visible on the photograph and the margins of the model coincide with the margins of the head. The cursor shows the position of the ear on the model, which is just to the rear of its position on the photograph. A specified region of the model defines the region of the head and neck from which the pattern sample is to be scanned. The horizontal line near the bottom edge of that region prevents the scan from extending past the edge of the frame or below the waterline.



The end product of the pair-wise comparison of all photographs is the assignment to each photograph of an “animal number”. Because the risk of falsely matching photographs of different animals is negligible, all photographs to which the same animal number has been assigned show the same animal. Whether different animal numbers definitely represent different animals depends on whether they are assigned to photographs that show the same side, whether those photographs were from the same session, the quality of photographs and the distinctiveness of the pelage pattern. Based on photographs that were “acceptable”, as defined above, the catalogue contains 4,879 animal numbers and hence a maximum of 4,879 different animals are represented. Of these, 1,797 are assigned to animals photographed only from the left, 2,301 to animals photographed only from the right and 781 to animals photographed from both sides. Thus if all the animals photographed only from the left also appear in photographs from the right the number of animals represented by the catalogue is 3,082. If the photographs are restricted to those in which at least 90% of the cell area is clearly visible and covered in distinctive markings, to be certain that they represent different animals, then the minimum number of animals in the catalogue is reduced to 1,671.

Moment estimators of population size

A common framework for modelling the recapture frequencies of individual tags (such as bird rings) can be accessed by presenting results as a matrix of individual “capture histories” (Lebreton *et al.* 1992). A capture history matrix provides a powerful and convenient way to analyse resighting frequencies, particularly since it can be analysed using software packages such as MARK (White and Burnham 1999) that provide access to a wide variety of models. Unfortunately, existing capture history models do not allow for individual identification based on photography of different body regions (for example, left and right sides of the head), nor do they incorporate the effect or errors in identification. We therefore adopted an ad hoc procedure, based on summing pairs of “release” and “recapture” samples, to derive moment estimators of local and total population size using a method suggested by Darroch (1961). Basically, the seals photographed in each area A to G on each sampling trip were treated as release samples to be “recaptured” (*i.e.* photographed again) during a later session in the same or a different area. The size of the population using the haul-outs in each area in the final year (2000) was then estimated by summing the results of all of those release/recapture experiments.

The release/recapture approach allowed problems relating to viewpoint, pattern and photo quality to be addressed in a relatively simple way. First some substandard photographs were removed from the data by specifying the maximum allowable angular deviation of the camera axis (65° from the normal to the pattern cell) and the maximum allowable percentage of the cell obscured (50%). That selection was therefore independent of pattern quality and involved no potential bias to particularly well-marked animals amongst the photographed seals. It resulted in a set of “include” photographs showing either the left or right side of the head. A subset of those photographs was then defined as “tagged”, *i.e.* with less than 10% of the cell obscured and showing distinctive pattern in an image of sufficient quality to ensure that it would match to any later “include” photograph of that seal taken from the same side. That selection did therefore depend on pattern quality but was only used in constructing the release samples. As the recapture samples were not restricted to photographs of the tagged type the resulting population estimates were not biased to well-marked animals. Thus, each left side “release” sample consisted of animals photographed in a given area during a given trip for which at least 1 tagged left side photograph existed from that or a previous trip. Right side releases were defined in the same way, exploiting the left to right matches recorded in the field to maximise the size of each release sample. As the recapture samples were not restricted to tagged photographs matches between photographs in the same sample could have been missed by the automated comparison procedure. Thus, to ensure that the sizes of the recapture samples were not overestimated, each was restricted to a single photographic “session” which, as described previously, had been subjected to careful pair-wise comparison by eye.

In the following notation “*s*” indexes the photographic trips undertaken to the Baltic grey seal haul-outs throughout the 1995 to 2000 period and “*t*” the sessions during year 2000 only. “*i*” and “*j*” index the 7 subregions (A to G) illustrated in Fig. 2 and “*v*” indexes the side of the head shown in the photograph, left or right.

$N_{i,s,v}$ the number of seals which were photographed during trip *s* in area *i*, either from

side *v* or only from the other side but known to have been previously photographed from side *v*.

$N'_{j,t,v}$ the number of seals photographed from side *v* during a subsequent photographic session *t* in area *j*.

$R_{ij,st,v}$ the number of seals which were photographed on trip *s* in area *i*, either from side *v* or only from the other side but known to have been previously photographed from side *v*, and photographed again from side *v* during session *t* in area *j*.

If we ignore for the moment any losses of marked seals over the period *s* to *t* then the expected number of recaptures, $R_{ij,st,v}$, is given by:

$$E[R_{ij,st,v}] = N_{i,s,v} m_{ij,st} N'_{j,t,v} / P_{j,t} \quad (1)$$

where $E[x]$ denotes expectation of *x*, $P_{j,t}$ is the number of seals in area *j* at the time of session *t* and $m_{ij,st}$ is the probability that a seal photographed in area *i* on trip *s* will be in area *j* at the time of session *t*. This is because $N_{i,s,v} m_{ij,st}$ is the expected number of seals photographed in area *i* on trip *s* that were in area *j* at the time of session *t* and $N'_{j,t,v} / P_{j,t}$ is the fraction of seals in area *j* that were included in the recapture sample.

Because we are assuming no losses over the period *s* to *t*, the sum over *j* of $m_{ij,st}$ must equal 1 for all *i* (for example, a seal photographed in subregion B during a trip in 1997 must be in one or other of subregions A to G at any given time in year 2000). Thus if we rearrange equation (1) to leave just $m_{ij,st}$ on the right of the equation and sum over the equations for areas *j* we obtain:

$$\sum_j (E[R_{ij,st,v}] / N_{i,s,v} N'_{j,t,v}) P_{j,t} = 1 \quad (2)$$

for each area *i*. Replacing $E[R]$ by R , this linear system of equations can be solved to provide moment estimators for the local population sizes $P_{j,t}$. Over a given interval *s* to *t*, these are also the maximum likelihood estimates for $P_{j,t}$ (Darroch 1961).

The local populations sizes $P_{j,t}$ are the “parameters of interest” here because they sum to form the total population size for grey seal in the Baltic and also provide an estimate of how that population is distributed (during the summer months).

More importantly, estimating local population sizes avoids bias in the total population estimate that would otherwise result from geographical variation in the proportion of seals photographed. The quotient $N'_{j,t,v} / P_{j,t}$ makes no reference to the release area i so its use in equation (1) rests on the assumption that the probability a seal is resighted is the same for all seals in area j at that time, irrespective of where they were previously. For a sufficiently small subregion that assumption is reasonable, both because variation in effort is reduced and because population mixing is increased within a small area. But the inevitable variation in sampling effort combined with uneven mixing over the Baltic as a whole means that the probability a seal is resighted is certainly not the same for all seals in the Baltic. A population estimate based on treating the Baltic as a single region would be biased, downwards if geographical variation in sampling effort was consistent between years and upwards if the sampling pattern changed over time.

The system of equations (2) refers to a single trip/session pair s and t . There are a large number of such systems, none of which could be solved individually because to do so would require release of seals from every area on trip s and an effort to recapture seals in every area during session t (to avoid any zero denominators on the left hand side of each equation). To obtain a solution the equations (1) were first added over different trip/session pairs and over left and right sides so that the sum of products of release and recapture samples $\sum_v \sum_{st} N_{i,s,v} N'_{j,t,v}$ was much greater than zero for each of the 49 area pairs. Only trip/session pairs with recapture sessions in year 2000 were used because that was the only year in which all areas were sampled. The equations were then rearranged, as before, to form a single set that was solved for the local population sizes in the summer of year 2000:

$$\sum_j (E[\sum_v \sum_{st} R_{ij,st,v}] / \sum_v \sum_{st} N_{i,s,v} N'_{j,t,v}) P_{j,2000} = 1 \quad (3)$$

for each area i .

To allow the parameters $m_{ij,st}$ and $P_{j,t}$ to be taken out of the summation meant assuming that the local population sizes were constant over the

sampling period in year 2000 (which seems reasonable given that sampling was restricted to the summer months) and that the probabilities $m_{ij,st}$ were constant at m_{ij} over any release/recapture interval. The latter assumption is reasonable if the probability of a seal moving from one area to another is determined by its preferences for each area and those preferences remain constant within the summer season and from one summer to the next. It also requires that the minimum interval between s and t is sufficiently long for the seal to have moved from its previous location so that its new location depends only on those preferences. If the k th of the P seals in the total population has constant preferences p_{ki} and p_{kj} for areas i and j then m_{ij} would equal $\sum_k p_{ki} p_{kj} / P_i$ independent of the time interval. Whether that is a reasonable model for seal movements during the summer is not known but with all areas sampled in only 1 year we did not have the option of letting the movement probabilities change over time. The only simple alternative, as used for example in the classified models available via program MARK, is to use Markov transition probabilities, where the movement of an animal to a new location depends only on its current location, but that is not appropriate for mammals that become familiar with certain areas during their development. In the preference model movement probabilities would depend on an animal's previous locations (although those are not used in the current analysis) but are independent of the time interval between release and recapture; in a memory-less Markov model the probabilities would be independent of previous locations but would depend on the interval.

The concept of a seal being "in" a particular subregion has not been defined and is a rather artificial one for seals that can move freely between haul-outs at any time of the year. One way to define it is to consider any moment in the cycle of successive haul-out and pelagic phases, such as the moment a hauled-out seal returns to the water. Then the number of seals "in" a region at a given moment could be considered as the number that will next return to the water from any haul-out in that region (as opposed to other regions of the study area and irrespective of whether the seal is already hauled-out at that moment or has yet to do so).

Losses from the population

There will inevitably have been losses from the marked population over the 6 years of sampling. If the size of the losses is known their effect can be simply incorporated by a proportional reduction in the expected number of recoveries. Thus in the denominators in equation system (3) we can include within the summation a term $S_m^{d(s,t)}$ where $d(s,t)$ is the time interval in years from trip s to session t and S_m is the probability of survival per year over that interval. Here “survival” means survival of the markings that permit identification. Losses could be of 3 types: permanent emigration of marked animals, death of marked animals and loss of some markings as young males become sexually mature and the pelage darkens. In the case of the Baltic we assume it is safe to ignore the first source of loss because of the small number of grey seals ever seen beyond the 7 regions.

To estimate the losses due to the remaining 2 sources we calculated Jolly-Seber (Seber 1982) estimates of survival from the Swedish haul-out data. The releases and recaptures were combined over the different haul-outs with left-side releases in a given year defined as animals photographed in that year for which a left-side tagged photograph was available in that or any previous year (right-side releases being defined similarly). The recaptures corresponding to each release sample were then the total number or resightings occurring at any time following the release year.

Selection by quality of pattern

Many seals in the population are not well marked and cannot be identified individually using photography of the head and neck. It would be inefficient to take photographs of such animals and probably impossible to prevent a photographer selecting well marked seals in a group to photograph, particularly if the group was large and time was short.

To correct for this prior selection of well-marked seals by the photographer, marking qualities were recorded in 2 ways. Firstly a large number of seals selected randomly at the haul-outs was scored by the photographer as having “good”, “medium” or “bad” markings. The proportions falling into each category were averaged over the different haul-outs, weighting by the number

of seals counted at each haul-out. Secondly the photographer allocated, into the same categories, a sample of the seals actually photographed. That scoring was done in the field, not by later examination of the photographs, to avoid confounding the effects of pattern and photograph quality. The photograph scores were included in the database so that when photographs were selected to form the release and recaptures samples the proportion of seals in those samples that were in each of the 3 categories could be determined.

The marking quality scores were used to derive a correction factor for selection by the photographer in favour of well-marked seals. Let C_g , C_m and C_b represent the proportions of seals with good, medium and bad markings in the whole population. Let $c_{g,i}$, $c_{m,i}$ and $c_{b,i}$ represent the proportions amongst the releases from area i , $c'_{g,j}$, $c'_{m,j}$ and $c'_{b,j}$ the proportions amongst the recapture samples in area j . Returning to equation (1), the expected number of recaptures, $R_{ij,st,v}$, can be stratified by pattern quality by multiplying $N_{i,s,v}$, $N'_{j,t,v}$ and $P_{j,t}$ by the appropriate values of c , c' and C . For example, the expected number of “good” recaptures depends on the number of “good” releases, the number of “good” seals in the recapture effort and the number of “good” seals in the population. If these equations are now summed over the 3 categories, the total expected recaptures in all categories is restored on the left hand side, and the proportions on the right appear as the quotients $c_{q,i}c'_{q,j}/C_q$ summed over the quality category q to generate a correction factor Q_{ij} for each pair of areas.

False negative errors in pattern matching

Grey seal patterns in the good or medium category are sufficiently complex for the risk of false positive or false negative matching errors to be negligible when photographs showing the entire head and neck region are inspected visually. When comparison is based on a small subregion, as required for the automated matching software, the risks can still be minimised by using only those photographs in which that subregion contains a sufficiently complex pattern, i.e. only tagged photographs. But restricting both release and recapture samples to tagged photographs would have biased the resulting population estimates so selection of photo-

Table 1. Statistics used to estimate annual survival from year $i-1$ to year i of identified seals. Identified seals may be lost from the catalogue by darkening of the pelage markings (in male seals) as well as mortality. The data are from Swedish haul-out sites only. Statistics with subscripts "L" and "R" refer to seals known from the left and right respectively by year i and are summed to give the unsubscripted statistics. r^i represents the number of recaptures in year i , m the number of releases in year i and r the number or recaptures of those releases in subsequent years. z is the number or recaptures of releases prior to year i that were not seen in year i . Thus $\frac{zm}{r}$ is an estimate of the number of marked animals alive in year i that were not seen in that year.

year i	m_L	r^i_L	Z_L	$\frac{Z_L m_L}{r^i_L}$	m_R	r^i_R	Z_R	$\frac{Z_R m_R}{r^i_R}$	m	r^i	$\frac{zm}{r}$	$\frac{r^i + z_i m_i / r_i}{m_{i-1} + z_{i-1} m_{i-1} / r_{i-1}}$
1995	72	0	0	0	86	0	0	0	158	0	0	-
1996	114	33	27	93	80	4	36	90	194	11	183	1.267
1997	236	63	32	120	272	30	38	138	508	58	258	0.838
1998	188	40	55	265	236	49	64	302	424	89	567	0.856
1999	217	58	36	355	401	91	43	479	618	149	756	0.913

graphs for the recapture samples had to rely on objective measures of photograph quality.

Some matches between seals in the release and recapture samples may therefore have been missed. False positive matches were eliminated by checking all potential matches by eye, using the original photographs that showed the entire

head and neck region. Overestimating the size of the release samples was avoided by restricting them to tagged photographs. Overestimating the size of the recapture samples was avoided by restricting them to photographs taken during a single session and comparing all photographs within a session by eye. But release to recapture photograph pairs that, on automated comparison, scored less than a threshold value were not subject to any further checks. There was therefore a risk that a pair of photographs of the same animal would not score above the threshold value and hence the presence of a released animal in the recapture sample be missed.

If the size of that risk were known its effect on the population estimates could easily be eliminated by a proportional reduction in the expected number of recaptures, just as for the losses from the marked population. Furthermore, given a sufficiently large sample of seals identified in a completely independent way, the risk of failing to identify a release via its pelage markings would be simple to evaluate. In the absence of such a sample we attempted to generate a test set using instances where a number of photographs showing the same seal in different postures and/or from different angles had been registered from the same session and where a seal was identified on 3 or more dates. Both those instances provide a number of photograph pairs exceeding the minimum number that must have been matched in order to provide the identification. The proportion of those additional pairs that fail to exceed the threshold value when compared by the software provides a measure of the risk of a false negative error for a photograph pair.

The risk of failing to identify a released seal in a recapture sample then depends on the number of photographs by which it was known as a release and the number by which it was known as a member of the recapture sample. If, for example, it was known by 2 photographs in each of the samples then failing to identify it requires that each of the 4 photograph comparisons that would be made by the software would have to score less than the threshold value. So if the probabilities of scoring less than the threshold value were considered to be independent for each of the 4 photograph pairs then the risk of failing to identify the released seal would be equal to the

risk of a false negative error for a single photograph pair taken to the fourth power. The risk of failing to identify a seal obviously declines very rapidly with an increase in the number of photographs by which it is already represented.

Using results from the test sets, the frequency distribution for the number of photographs by which each animal in the catalogue is currently represented and assuming independent probabilities of false negative errors for each photograph pair we estimated an average 2% risk of failing to identify a released seal in a recapture sample. However that result is not very reliable, for example photographs from the same session, though differing in viewpoint and posture, will be similar in lighting and the state of the pelage and may thus fail to provide a realistic test. Instead of attempting to correct the population estimates for missed matches we therefore decided to regard this as a source of positive bias in the estimates.

The results presented below were thus based on solution of the following set of equations that incorporate correction factors for losses from the marked population and for selection in favour of well-marked seals by the photographer but not for the risk of missing released animals in the recaptures samples:

$$\frac{\sum_j (E[\sum_{st} R_{ij, st, v}]) / Q \sum_{st} S_m^{d(s,t)} N_{i, s, v} N'_{j, t, v}}{P_{j, 2000}} = 1 \quad (4)$$

for each i .

Approximate 95% confidence limits were derived by simulating variation in the recapture frequencies used to derive the estimates. Because of summation over sessions some of the recapture “frequencies” represented by R_{ij} exceed the number of different seals actually recaptured between those areas over those intervals. The actual number of different seals involved in each case was used as the rate parameter of a Poisson distribution. One value was generated at random from each Poisson distribution and scaled up by the ratio of R_{ij} to the number of different seals recaptured. Those scaled random values then replaced R_{ij} in the calculation of the population estimates. The procedure was repeated 1,000 times to generate 1,000 different sets of population es-

timates and the 2.5% and 97.5% percentiles of the estimate distribution, $P_{2.5}$ and $P_{97.5}$, recorded. Approximate 95% lower and upper confidence limits were then calculated as $\mu^2/P_{97.5}$ and $\mu^2/P_{2.5}$ where μ represents the point estimate.

RESULTS

Losses from the population

Table 1 gives the statistics for left and rights sides, and for left and right sides combined, for each year from 1995 to 1999. The effect of the low number of recoveries from 1996 releases is evident in the survival estimate for 1995 to 1996 exceeding 1. Combining the statistics over the years gave an estimate of 0.9035 for annual survival from 1995 to 1999 (it is not possible to derive an estimate for the 1999 to 2000 survival). We used that value to calculate the year 2000 population size point estimate, however as the data were restricted to a subset of the Swedish haul-outs we can not be certain that this value is applicable to the whole Baltic.

Selection by quality of pattern

The proportions of seals randomly selected at Baltic sites that were allocated to the “good,” “medium” and “bad” pattern quality categories were 0.395, 0.17 and 0.435 respectively. Very similar proportions (0.4, 0.15 and 0.45) were independently assessed for an earlier analysis of grey seal photo-id data from the North Sea (Hiby 1994). Thus most seals appear to be either distinctively marked or hardly marked at all, both in the Baltic and North Sea. Adult males make up most of the seals with “bad” markings, suggesting that the loss of male markings occurs over a short period of time. The remainder was mostly very young seals.

Combining the proportions for randomly selected seals with those for the photographed seals gave a correction factor, Q , of 2.27 – the same factor was used in all areas because the same photographer took most of the photographs and demonstrated the data collection methods to the other photographers.

Moment estimators of population size

The majority of resightings occurred in the same area where the seals were originally photographed (Karlsson *et al.* 2005). Table 2 shows

Table 2. Total number of different grey seals recaptured in each area of the Baltic in year 2000 that were released from each area in years 1995 to 1999 or during an earlier trip in year 2000.

areas	A	B	C	D	E	F	G
A	6	2	0	0	0	1	0
B	1	28	7	3	1	1	1
C	0	8	62	14	11	2	0
D	0	2	9	44	8	1	0
E	0	0	8	9	98	1	0
F	2	3	4	2	1	10	0
G	0	1	0	0	0	0	7

Table 3. Point estimates and confidence intervals for the number of grey seals of both sexes and all ages using the summer haul-outs in areas A to G of the Baltic in year 2000.

Areas	estimate	lower 95% limit	upper 95% limit
A	781	179	*
B	3,203	2,017	9,562
C	4,096	3,070	5,338
D	842	502	1,878
E	2,121	1,748	2,513
F	1,619	720	*
G	2,969	1,359	4,827
All areas	15,631	10,940	17,989

* upper 95% confidence limits for areas A and F were not available by the method used; upper 80% limits were 2,660 and 3,687 respectively

the number of resightings in year 2000 of seals seen in earlier years or during an earlier trip in year 2000. Using equation (4) with those data gave the local and total Baltic grey seal population estimates for year 2000 in Table 3.

The confidence limits presented in Table 3 are very wide for the local population sizes, as might be expected given that it was only possible to use recapture samples in the final year of survey. The limits for the total Baltic population size are much narrower but as they appear in Table 3 they fail to incorporate errors in the estimation of Q and S_m . We calculated a coefficient of variation (CV) of 0.05 for the estimate of Q by assuming a multinomial distribution for the numbers of seals from the random haul-out samples that were allocated to the 3 pattern quality classes. Combining this with

the CV of 0.115 corresponding to the confidence limits in table 3 increases the CV for the total population estimate to 0.125, *i.e.* by about 9%.

Part of the uncertainty concerning S_m stems from the fact that it was estimated using data from a subset of Swedish haul-outs and, as it is not possible to express uncertainty about that component of the error as a CV, we chose instead to recalculate the population size estimate using lower and upper bounds on S_m . As a lower bound on the survival of marks we used the estimate of 0.85 from the analysis of North Sea grey seal photo-id data (Hiby 1994) because it includes an emigration component, which is assumed to be negligible for the Baltic study. As an upper bound we used an estimate of 0.95, which is the current adult female survival estimate derived from monitoring surveys of UK grey seals (Hiby and Duck, submitted). That value is consistent with calculations prepared for the Baltic grey seal management plan (Anonymous 2001) and includes neither emigration nor the loss of markings by male seals. Those recalculations then reduced the lower limit on the estimate of the year 2000 population size to 9,592 and increased the upper limit to 19,005.

DISCUSSION

The point and interval estimates derived from our photo-id study can be compared with counts of moulting haul-outs conducted from 2000 to 2004 (Halkka *et al.* 2005). The count of 9,700 seals during the moult from late May to early June of 2000 is much smaller than our photo-id point estimate of 15,631 for the summer of that year and only slightly larger than the lower 95% confidence limit of 9,592 seals. We would of course expect the count of moulted animals to be smaller than our estimate of the population size, because only a part of the population will be hauled out at any one time.

2000 was the first year with combined effort all over the Baltic to survey grey seals during the moult. Such combined survey efforts in the Baltic have been repeated annually since then and the numbers of animals counted were 10,300 in 2001, 13,100 in 2002, 15,950 in 2003 and 17,640 in 2004 (Halka *et al.* 2005). A population increase from 9,700 to 17,640 over 5 years would

have required immigration, which is inconsistent with the closed nature of the Baltic population, hence the later counts must have included a bigger proportion of the population. Standardized annual counts at all major haul-out sites along the Swedish Baltic coast from 1990 to 2004 indicate an average annual growth rate of approximately 7.5% (Karlsson and Helander 2005). Using our photo-id estimate for year 2000 and applying an annual increase rate of 7.5% gives a projected point estimate in 2004 of 20,875, with 95% confidence limits from 12,810 to 25,380. Comparing these values with the count at moulting haul-outs in 2004 suggests that 70% - 85% of the population is hauled out at that time.

The estimate of population size is not fully efficient given its dependence on the summation of release/recapture sample pairs rather than the full capture history of each seal. One general area that needs further work is the development of more efficient estimators that can allow for problems inherent in photo-id data such as selectivity and the risk of failing to identify animals, both related to pattern and photo quality. Another problem related more specifically to this study is its dependence on haul-out behaviour during the summer months. In this regard there is a potential bias in the population estimate that has not been addressed in the above results. By sampling for pattern quality at the haul-outs we estimated and allowed for selectivity by the photographer in favour of well-patterned seals. However it is possible that the proportion of well-patterned seals at the haul-outs is not representative of that proportion in the population as a whole. For example, poorly-patterned juvenile seals might be under-represented at the summer haul-outs. Similarly, males might be under- or over-represented.

REFERENCES

- Anonymous, 2001. Nationell Förvaltningsplan för Gråsälsbeståndet i Österjön (Management plan for Grey Seal in the Baltic). Naturvårdsverket (Swedish Environment Protection Agency). 83 pp. (In Swedish).
- Bergman, A. 1999. Health condition of the Baltic grey seal (*Halichoerus grypus*) during two decades. Gynaecological health improvement but increased prevalence of colonic ulcers. *APMIS* 107:270-282.

The potential to address these problems is limited. The proportion of juveniles at the haul-outs might be compared with population models but then it is not known at what age seals enter the well-patterned component. Reliable estimates for the proportion of males in the population are not available at all. It is worth noting that alternative methods of estimating population size are subject to the same problems, for example, those based on census of newborn pups do not provide any estimate of the number of adult males.

The annual survival rate of 0.9035 estimated from this study is not directly comparable to previous estimates because of the loss of marks among male seals. However, it should be possible to obtain a revised estimate from photo-id samples obtained well after year 2000. Resightings of seals first identified in or before year 2000 will all be of adult females because the pelage of any young males included in the original samples will by then be too dark to recognize. Thus, survival estimates derived from later samples will be for adult females only and hence comparable to those from previous studies (e.g. Harwood and Prime 1978, Schwarz and Stobo 2000).

ACKNOWLEDGEMENTS

This project was funded with grants from the Swedish World Wide Fund for Nature/ WWF Sweden, the Swedish Environment Protection Agency and from the Swedish Project "Sälar och Fiske" ("Seals and Fisheries") to Björn Helander at the Museum of Natural History in Stockholm. We thank Gunilla Hamne, Erik Isaksson, Peter Lögdberg, Erik Rehnström, Håkan Sahlin and Lars Wallin for field assistance.

- Bergman, A. and Olsson, M. 1985. Pathology of Baltic grey seal and ringed seal females with special reference to adrenocortical hyperplasia: is environmental pollution the cause of a widely distributed disease syndrome? *Finn. Game Res.* 44:47-62.
- Bigg, M.A. 1982. An assessment of killer whale (*Orcinus orca*) stocks off Vancouver Island, British Columbia. *Rep. int. Whal. Commn* 32:655-666.
- Clapham, P.J. and Mayo, C.A. 1990. Reproduction of humpback whales (*Megaptera novaeae gliae*) observed in the gulf of Maine. *Rep. int. Whal. Commn*, Special Issue 12:171-176.
- Darroch, J.N. 1961. The 2-sample capture-recapture census when tagging and sampling are stratified. *Biometrika* 48:241-60.
- Halkka, A., Helle, E., Helander, B., Jüssi, I., Jüssi, M., Karlsson, O., Soikkeli, M., Stenman, O. and Verevkin, M. 2005. Numbers of grey seals counted in censuses in the Baltic Sea, 2000-2004. Abstract. Symposium on the biology and management of seals in the Baltic Area. 15-18 February 2005, Helsinki, Finland, 16-17.
- Harding, K.C. and Harkonen, T.J. 1999. Development in the Baltic grey seal (*Halichoerus grypus*) and ringed seal (*Phoca hispida*) populations during the 20th century. *Ambio* 28: 619-627.
- Harwood, J. and Prime, J.H. 1978. Some factors affecting the size of British grey seal populations. *J. Appl. Ecol.* 15:401-411.
- Hiby, L. 1994. Abundance estimates for grey seals in summer based on photo-identification data. In: Hammond, P.S. and Fedak, M.A. (eds.); *Grey seal in the North Sea and their interactions with fisheries*. Sea Mammal Research Unit. Final report to the Ministry of Agriculture, Fisheries and Food under contract number MF 0503, 5-22.
- Hiby, L. and Duck, C.D. Estimates of the size of the British grey seal *Halichoerus grypus* population and levels of uncertainty. *J. Appl. Ecol.*, submitted.
- Hiby, L. and Lovell, P. 1990. Computer aided matchings of natural markings: a prototype for grey seals. *Rep. int. Whal. Commn*, Special issue 12:57-61.
- Karlsson, O. and Helander, B. 2005. Development of the Swedish Baltic grey seal stock 1990-2004. Abstract. Symposium on the biology and management of seals in the Baltic Area. 15-18 February 2005, Helsinki, Finland, 21 pp.
- Karlsson, O., Hiby, L., Lundberg, T., Jüssi, M., Jüssi, I. and Helander, B. 2005. Photo-identification, site fidelity and movement of female of Gray Seals (*Halichoerus grypus*) between haul-outs in the Baltic Sea. *Ambio* 34:628-634.
- Lebreton, J.G., Burnham, K.P., Clobert, J. and Anderson, D.R. 1992. Modelling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecol. Monogr.* 62(1):67-118.
- Schwarz, C.J. and Stobo, W.T. 2000. Estimation of juvenile survival, adult survival and age-specific pupping probabilities for the female grey seal (*Halichoerus grypus*) on Sable Island from capture-recapture data. *Can. J. Fish. Aquat. Sci.* 57:247-253.
- Seber, G.A.F. 1982. *The estimation of animal abundance and related parameters*. 2nd edn. Macmillan, New York, N.Y.
- White, G.C. and Burnham, K.P. 1999. Program MARK: Survival estimation from populations of marked animals. *Bird Study* 46:120-138, Supplement.

Würsig, B. and Würsig, M. 1977. The photographic determination of group size, composition and stability of coastal porpoises (*Tursiops truncatus*). *Science* 198:755-756.