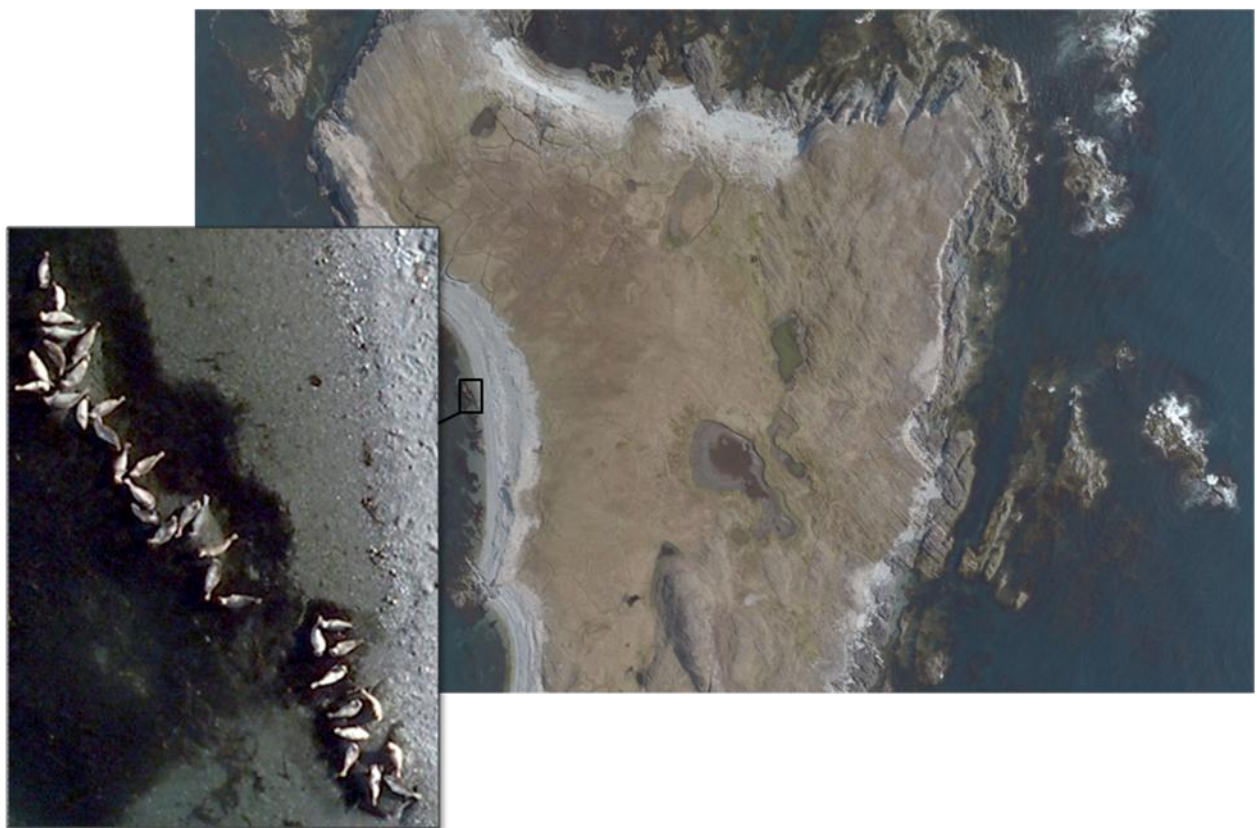


The world's northern most harbour seal population - How many are there?



Benjamin Merkel

BIO-3910 Master's thesis in Biology

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Front page photo: One of the 2950 aerial digital stereoscopic images counted in this study, with a magnified inset showing a group of hauled out harbour seals *Phoca vitulina vitulina*.

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Preface

This thesis has been written as an article, for submission to the journal “PLOS ONE”. The manuscript has thus been prepared according to the “Manuscript Guidelines” for this journal.

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Benjamin Merkel

Abstract

This study presents the first abundance estimate for the world's northernmost harbour seal (*Phoca vitulina*) population, which resides in Svalbard, Norway, based on three digital stereoscopic photographic surveys conducted in 2009 and 2010. The counts from these high resolution 3D images were combined with a novel method for estimating correction factors for animals that were in the water at the time of the surveys, in which extensive behavioural data from radio-tagged harbour seals were used together with a modelled stationary age structure to estimate the proportion of seals of various age and sex classes hauled out at the times of the surveys. To detect possible seasonal shifts in age distribution between surveys, lengths of hauled out seals were measured from the stereoscopic images. No such length differences were detected; but, this may be due to a high degree of sexual dimorphism exhibited in this population. Applying the modelled correction factors, a total of 1888 (95 % CI: 1660-3023), 1742 (1381-3549) and 1812 (1656-4418) harbour seals were estimated for the surveys flown on 01 August 2009, 01 August 2010 and 19 August 2010, respectively. The similarity between the three survey estimates (despite significant differences in the number of animals actually counted on the photos from each survey effort) suggests that the variation in numbers of hauled out seals is reasonably accurately adjusted for by the correction factor model. The low population size, the limited spatial distribution of the population and its reduced genetic diversity make it vulnerable to stochastic mortality events. However, barring disease events, climate change—a major threat to many arctic marine mammals—is likely to have a positive impact on this population as more suitable habitat becomes available and competition from endemic arctic pinnipeds is reduced.

Introduction

Harbour seals have a broad geographic distribution in coastal waters in the northern hemisphere. The species is categorized into five subspecies, with *Phoca vitulina vitulina* occupying the eastern Atlantic from Brittany to the Barents Sea, including the world's northern most population located in the high Arctic archipelago of Svalbard (78.2°N, 15.5°E), Norway [1]. Harbour seals were first reported to occur in this island group in 1898 [2], but were not the subject of scientific study until the 1970s (reviewed in [3]). The harbour seals in Svalbard constitute a highly genetically distinct population that has limited gene flow and low genetic diversity; this population also displays evidence of having experienced a recent bottleneck [4].

The Svalbard harbour seal population exhibits a high degree of sexual dimorphism compared to more southerly populations with adult males being significantly heavier and longer than adult females [5]. There is also a marked absence of older individuals in this population; the oldest seal registered in an extensive capture programme in the late 1990s was only 22 years old. This lack of older animals is unusual compared to other populations of this species, which have a much higher proportion of individuals in the 15+ yr age categories [6,7,8,9,10]. Svalbard harbour seals are on the Norwegian Red List and are protected from hunting. Some crude attempts to enumerate this population have been conducted [1,3], based on counts made from land or sea, but no complete abundance estimate is available.

The most common method for estimating abundance of harbour seals is to count the number of animals ashore during the pupping or moulting periods. Hauled out seals are often counted either directly (e.g. [11,12,13,14,15]) or on photographs from aerial surveys (e.g. [16,17,18,19,20]). The pupping period for harbour seals in Svalbard takes place during the second half of June [21]. Harbour seals usually give birth to a single pup with an adult-like pelt; although a small proportion of pups of this species are born bearing their lanugo coats [22]. Pups are nursed for about 24 days [23] and subsequently weaned around mid July. Harbour seals are able to swim and dive from the day they are born and gradually increase the time they spend in the water with age [24,25]. Towards the end of the nursing period mature females enter breeding condition and mating occurs, which takes place in the water [26,27,28]. Moulting follows the breeding period, taking place from mid July to mid

September. The moulting process in individuals takes three to five weeks to complete [29]. Immature seals moult first, followed by adult females, and lastly adult males [29,30,31].

The pupping and moulting periods constitute the time of the year when the highest proportion of harbour seals is hauled out on shore and thus represents the best times to conduct population surveys. However, even during the peak moulting period there is always a proportion of the population at sea and therefore not visible for counting. Several studies have shown that this proportion varies with temporal and environmental conditions such as; season, time of the day, tidal cycle and various meteorological factors (e.g. [29,31,32,33,34]). Because of differences in the timing of moult according to sex and age, the proportion of the population counted might not be representative of the sex and age structure of the total population [35]. This natural variation in number of seals hauled out, as well as the age and sex composition of the hauled-out proportions of the population must be taken into consideration during population assessments.

Harbour seals have a restricted distribution within the Svalbard Archipelago. The main haul-out area for this population during pupping and moulting is the west coast of Prins Karls Forland [1]. Pupping has in fact only been observed along this 86 km long coast line [3]. Additionally, a satellite tagging study conducted 1992-1994 [36] concluded that the majority of Svalbard's harbour seals appeared to be quite stationary around Prins Karls Forland throughout the year.

The purpose of the present study was to provide the first population estimate for harbour seals occupying Prins Karls Forland, using a series of aerial surveys (counting seals on digital stereoscopic photographs), in combination with correction factors based on both behavioural data (haul-out information from VHF tracking) and environmental data in combination with information on population age structure (based on catch data).

Methods

Ethics statement

All research activities conducted during, and in support of, this study were carried out under permits from the Norwegian Animal Care Authority and the Governor of Svalbard (2009/00103-2 a.512) and followed best practice for all animal handling [37].

Aerial surveys

Aerial digital photographic surveys were flown for harbour seals, covering the entire west coast of Prins Karls Forland (Figure 1), on 01 August 2009 and 01 and 19 August 2010. All of the surveys were flown during afternoon low tide periods, under similar meteorological conditions (sunny, no wind, no clouds). Since these are optimal haul-out conditions for this species [12,31,33,34], it is expected that a maximal fraction of the population was hauled out at the time of the surveys.

A Twin Commander 690C fixed-wing aircraft equipped with a Microsoft Vexcel Ultracam XP (Focal length: 100.5 mm; gyro mount with 5 % correction in pitch/roll and 20 % correction in yaw; software for image processing: OPC and ULTRAMAP (VEXCEL, Boulder, Colorado, USA)), flew the surveys at an altitude of 670 m. The flight plan was designed to cover the whole west coast of Prins Karls Forland including adjacent small islands and skerries (Figure 1). An image was shot approximately every two seconds while flying at 300 km/hr. Each image covered 0.31 km², so that an overlap of 60 % between each image was achieved to make stereoscopic visualization possible. In total 2,950 digital stereoscopic images, with a ground sample distance (i.e. pixel size) of 4x4 cm, were manually inspected for the presence of harbour seals using Z/I Imaging Quick View 4.2.0.1 software (Z/I Imaging GmbH, Aalen, Germany). The 01 August 2009 survey (975 images) was double-blind counted in 2D as well as in stereo by two readers to test for potential reader biases. Seals were relatively easily detected on the digital images and it was possible to distinguish harbour seals from other pinniped species on the images *i.e.* bearded seals (*Erignathus barbatus*) without difficulty (mainly by size). Variation in the number of harbour seals detected by the two different readers was deemed small enough to be insignificant (max. 3.3 %) and therefore no attempts were made to correct for reader bias. The small difference that did occur between

readers was mainly due to uncertainty in counts in a few cases where seals were disturbed and had rushed into the water at the time of the survey. Thus, for further estimations of population size it was assumed that all seals hauled out at the time of the surveys were detected and correctly identified to species.

To explore whether age structure of hauled out seals shifted through the moulting period, two surveys, 2.5 wks apart were flown in the second year of the study. The stereoscopic images enabled measurements of all non-moving seals in the images, including corrections of these measurements to adjust for angles of the substrate the seals hauled out on using SOCET SET 5.5 software (BAE Systems, California, USA). This made it possible to assess a potential shift in age structure through the moulting season via exploring the length distribution of the hauled out animals. Quantile-quantile plots were used to compare the length distributions of the seals between the different surveys.

Behaviour data

In order to be able to create an estimate of the harbour seal population at Prins Karls Forland, the number of seals hauled out during the surveys had to be divided by the estimated proportion of the various age and sex classes hauled out at the time of the surveys, to account for the proportion of animals in different age and sex categories that were in the water. A detailed data set on haul-out behaviour of Svalbard harbour seals was used to facilitate these calculations. Raw data for this estimate were collected during an earlier study on haul-out behaviour of this population [31]. In this earlier study the behaviour patterns of 37 harbour seals equipped with VHF tags (Followit AB, Lindesberg, Sweden) during the pupping and moulting season in 2000 (June to August) were monitored around the clock *via* three automatic receiver stations distributed along the western shoreline of Prins Karls Forland. The raw data from [31] was used to construct a model to predict the proportion of seals hauled out on any given day, time of day, time within tide cycle, and temperature. Due to the marked differences in haul-out behaviour of adult females, adult males, immature individuals and pups of the year [31], a correction factor, for each of these four groups was estimated. The VHF data was filtered by pulse rate using only pulses with ~ 1.5 sec intervals for all groups except adult females, where intervals of ~ 1.1 sec were retained in the dataset (similar to [38]). Signals were pooled into one hour bins since the 15 min resolution of the receiver scanning of the tags led to computational problems

during the model selection process. The time frame for the behavioural component of the study was 07 July to 25 August, because 07 July was the first day when there was no human disturbance (e.g. seal capture work) taking place in the study area and 25 August was the last day a signal was recorded. Records for individual animals went from 07 July to the last day upon which a signal was received for each of the individuals respectively. Six seals were excluded from the analyses because no signals were recorded for them. Consequently, haul-out data from 31 individuals (seven adult females, six adult males, eight juveniles and ten pups) were used as the basis to model a correction factor in this study. The haul-out behaviour of these seals is assumed to be representative for the population as a whole. Tidal data was retrieved for Ny-Ålesund (Figure 1) from the Norwegian mapping authority (<http://www.vannstand.no>). Temperature data for 2000 were taken from the weather station at Isfjord Radio (Figure 1) (<http://www.eklima.no>). Only ambient temperature values for the 01 August 2010 aerial survey were available. Therefore, the average of the temperature values from two weather stations in Longyearbyen and Ny-Ålesund (Figure 1) were used for the other surveys. This seems to be quite accurate as the calculated average temperature value for the 01 August 2010 survey only differed by 0.5°C from the observed value. For statistical analyses and model computations R software version 2.15.1 (R Development Core Team, 2012) was used.

Data analyses

A generalized additive mixed effect model (GAMM) using the “mgcv” package (version: 1.7-18) [39,40] was computed to estimate the proportion of time seals in each of the four age/sex groups hauled out. Due to the binary nature of the response variable (presence-absence) a binomial distribution was assumed and a logit-link was utilized. Further, a first-order autoregressive correlation structure (AR1) at the level of the data [41], together with a random inter-individual variance component, was incorporated to account for the autocorrelation and the individual differences in haul-out behaviour between tagged seals. A gamma value of 1.4, to avoid over-fitting, as recommended in [39], and restricted maximum likelihood estimation (REML) were used to estimate parameters of the models. Data for each covariate was standardised by subtracting the mean and then dividing by the standard deviation to unify the scale of all variables in order to prevent computation problems, as recommended in [42]. Exploratory gam plots were used to assess the relationship between

the response and each covariate. No strong co-linearity between predictor variables was found. The effect of day of the year (i.e. seasonal effects, DOY), time to and from the nearest low tide (LOW TIDE), time of the day (TIME), and air temperature in °C (TEMP) were examined in candidate models because of their documented effects on harbour seal haul-out behaviour [29,31,32,33,34]. All were included as continuous variables that varied for each of the four age/sex groups. Cubic spline regression smoothing functions were applied to DOY and LOW TIDE, with initial values for k of $k=5$ and $k=4$, respectively. A cyclic cubic spline regression smoothing function with initial $k=5$ was also applied to TIME to ensure circularity of the covariate [39]. TEMP was included as a linear effect.

Model selection for fixed effects terms was based on backwards selection. Explanatory variables were explored for significance (p value >0.05) sequentially [39,43].

The average TIME, LOW TIDE and TEMP values for the three hours in which each aerial survey took place were used to predict the proportion of seals hauled out for each of the four age/sex groups. A stationary population structure, based on catch data from a previous study [5], was used to combine the four estimates. Because juveniles were underrepresented in the data set [5], a linear model on a log scale was computed, based on an assumed 50 % pup mortality. A sex ratio for adult seals of 1:1 was assumed and data from age classes six to 22 years were included in the model. The correction factors (p) for each age/sex group (j) for each survey at time (t) were multiplied with the proportional representation of each group in the population (q) in order to derive an average population correction factor. The total population estimate (N) based on the aerial counts (Y) for each survey was then calculated using:

$$N_t = \frac{Y_t}{\sum (p_{jt} * q_j)}$$

In order to estimate the uncertainty in the population estimate, a non-parametric bootstrapping approach was used. Individual seals for each age/sex group were sampled with replacement 500 times. This gave a series of bootstrapped estimates, which combined with the observed counts at each time point, resulted in a set of population estimates. The 95 % quantiles of these estimates were used to derive upper and lower confidence bounds for the predicted population estimates.

Model validation was achieved by averaging residuals for each individual seal and each covariate and exploring violation of model assumptions (i.e. homogeneity of variance, non-linear relationships). All assumptions were met.

Results

A total of 2,950 digital stereoscopic images were inspected for seals both in 2D and in stereo. In all 981, 730 and 1295 harbour seals were counted on the images from 01 August 2009, 01 August 2010 and 19 August 2010 surveys, respectively (Table 1). The counts obtained using stereo imagery were higher (except for the 01 August 2010 survey), had less misidentifications and had more similar accuracy for both readers, compared to counts attained from 2D images (Table 1). More seals were detected, in the 19 August 2010 survey compared to those flown 01 August in either of the two study years. Haul-out groups in the northern part of Prins Karls Forland, as well as along the southern tip of the island, were larger later in the season (Figure 2).

A small fraction of seals were disturbed in each survey effort. Generally these movements toward the water were observed at the same geographical areas in each survey (Figure 2). One identified disturbance factor was the presence of a polar bear (*Ursus maritimus*) near the northern most haul-out group, at Fuglehuken, during the 01 August 2010 survey (red arrow in Figure 2). The fraction of disturbed seals was highest in this survey (Table 1).

The average measured lengths of harbour seals hauled out during the 01 August 2009, 01 August 2010 and 19 August 2010 surveys were 1.19 m (SD: 0.18 m, range: 0.63-1.63 m, N: 903), 1.20 m (SD: 0.18 m, range: 0.69-1.64 m, N: 477), and 1.18 m (SD: 0.17 m, range: 0.58-1.69 m, N: 1187), respectively. No temporal trend in length distribution could be detected between the three surveys (Figure 3).

All temporal and environmental parameters (DOY, TIME, LOW TIDE, and TEMP) were significant and hence they were all retained in the final model (Table 2, Figure 4). Figure 4 shows that the effect of DOY for adult females and juveniles were extrapolated towards the end of the study period since no data was available for this period (shaded areas in panel A and I). Estimated auto correlation between seals was 0.66 (SE: 0.026) and the between seal standard deviation on a logit scale (δ) was estimated to be 0.56 (SE: 0.102). There was no evidence for over dispersion. Estimated proportions of hauled out seals differed for each seal group and each survey (Table 3). The observed air temperatures during the VHF study period ranged from 0.5° to 10.5°C, encompassing the range experienced during the survey efforts.

The population structure model (R^2 : 0.87) estimated pup mortality to be 37 % while each subsequent year class had a mortality rate of 21 % (Figure 5). Using this age structure and an assumed 1:1 sex ratio for adult individuals the age composition of the population was estimated to be 24.7 % pups, 45.8 % juveniles and 14.8 % for each sex among adult animals (Table 3).

Combining the estimated proportions of hauled out seals for each group with the stationary age structure, correction factors of 1.92 (CI: 1.69-3.08), 2.39 (CI: 1.89-4.86) and 1.40 (CI: 1.28-3.41) for the three surveys, respectively, were achieved. These results, in combination with the aerial survey counts of the harbour seals at Prins Karls Forland produce total population estimates of 1888 (CI: 1660-3023), 1742 (CI: 1381-3549) and 1812 (CI: 1656-4418) for 01 August 2009, 01 August 2010 and 19 August 2010, respectively (Table 3).

Discussion

The results presented herein provide the first complete population estimate of the Svalbard harbour seal population. Earlier abundance information for this population was based only on opportunistic counts, no attempt had been made to correct for individuals that were in the water at the time of the survey [1]. The correction factor model in the current study, developed together with the modelled stationary population structure, gave a series of three quite similar population estimates (1742, 1812 and 1888) for the three aerial surveys conducted in two consecutive years, with the favoured estimate being 1888 (CI: 1660-3023) harbour seals residing along the west coast of Prins Karls Forland (see below).

Reader bias during inspection of survey images was considered small enough to be ignored in this study. The small differences that did occur between the readers were derived mainly from the uncertainty in counts of disturbed individuals that had fled into the water. Viewing the images in stereo generally increased the number of seals detected as well as reducing misidentification of seals and surrounding rocks compared with what was found in the 2D digital images; this was the case for both readers. Individual harbour seals were easily identified using the stereoscopic digital photographs. The 3D images enhanced the visibility of the shape of seals, increasing the contrast between them and the background rocks. The decrease in numbers from 2D compared to 3D count in the 01 August 2010 survey can be attributed to the large fraction of disturbed seals (Table 1), which made accurate counting difficult.

The number of seals counted on the images within each survey varied. In part this was due to varying environmental conditions, but also varying amounts of disturbance in each survey. Disturbance was highest during the 01 August 2010 survey in part because of the presence of a polar bear at Fuglehuken (Figure 2), a major haul-out site, which is normally occupied by a large number of harbour seals during favourable conditions, as seen in the other two surveys conducted in this study (Figure 2). Other possible sources of disturbance include the noise or shadow of the survey plane. However, the survey altitude (670 m) was sufficiently high that noise from the aircraft should not have had an impact on the behaviour of the seals. Various other studies using aircraft flying at lower altitudes (100 to 300m), report no specific disturbance to the normal haul-out behaviour of harbour seals from the passing aircraft [11,12,13,14,15,16,17,18,19,20,44,45]. Stochastic disturbances of harbour seal

groups do routinely occur without specific apparent external stimuli. These random events occur frequently among the Prins Karls Forland harbour seal haul-out groups, with sudden rushes into the water occurring without any apparent cause (personal observations). This common behavioural trait in this species makes repetitive surveys essential for accurate abundance determinations [20,46]. This is true even for populations that are largely unaffected by human disturbance, such as the isolated population in this study, that breeds and moults in a Nature Reserve where human access is very restricted. Because of the presence of the polar bear and the high fraction of disturbed seals in the 01 August 2010 survey for whatever combination of reasons, no attempt was made to estimate interannual differences between the surveys flown on 01 August of the two survey years. The fraction of disturbed seals during the first and third survey was small enough that the counts obtained during these survey efforts are assumed to represent precise, representative pictures of the number of hauled out harbour seals early and late in the moulting period, respectively and hence document seasonal variation adequately.

More seals were hauled out later in the moulting season (19 August 2010, 1295 seals) compared to earlier (01 August 981 & 730 seals in 2009 and 2010, respectively). An increase in hauled out individuals was observed particularly in the northern part of Prins Karls Forland and around the southern tip of the island (Figure 2). This suggests that these areas are mainly used by moulting seals while the more central regions around Forlandsøyane are known to be the main pupping and nursing areas [31].

Measurement on seals from the stereoscopic digital images was only possible for animals that did not move during the two seconds it takes for the camera system to construct overlapping images. For motionless animals it was possible to determine approximate body lengths, correcting lengths in relation to the angle of the substrate the animal was hauled out on using the 3D perspective afforded by the stereo images. Assuming that the fraction of seals measured in each survey represents the real size distribution for each respective survey, no difference in length distribution was detectable between the surveys (Figure 3). This suggests that there were no age structure differences between surveyed years or seasons. However, since the Svalbard harbour seals are sexually dimorphic with regard to size [5] a potential change in age distribution could be camouflaged since immature males could be mistaken for adult females and vice versa. In addition, the resolution of the images of 4x4 cm could be too low to detect subtle changes in the length distribution of the seals.

The model underlying the estimated correction factor mirrored the general knowledge of harbour seal haul-out behaviour, with peak haul-out times in the afternoon, right before or during low tide with an increasing probability of hauling out with increasing temperature [12,31,32,33,34]. Further, juveniles were observed to increase the amount of time hauled out first, which coincides with normal behaviour during moulting. These were followed by adult females and adult males, while pups gradually decreased the amount of time they spent hauled out through the study period (Figure 4) [31,35]. Towards the end of the study period, a lack of data for juveniles in particular, but also adult females, led to extrapolation of the model (shaded areas in Figure 4). This is probably the reason for the high estimate (90 %) produced for the proportion of juvenile seals hauled out during the last survey (Table 3), which is likely an overestimate for this age class. This issue is also reflected in the increased uncertainty around the population estimate for this survey (CI: 1656-4418). It is not surprising that the model provides the most accurate correction factors within the available range of the raw data.

Despite the differences in the numbers of seals counted during the three surveys, the adjusted population estimates (Table 3) are quite similar across all surveys. This indicates that the variation in the number of seals due to the different environmental and timing factors (e.g. difference in TEMP and TIME between the first and the second survey) is accurately adjusted for by the correction factor model. However, the 01 August 2009 estimate (1888 CI: 1660-3023) is thought to be the most reliable estimate, since the 01 August 2010 survey suffered from disturbance by a polar bear at an important haul-out location, and the correction factor for the 19 August 2010 survey was more uncertain due to lack of behavioural data for some age group this late in the season.

The raw data used to compute the stationary population structure was based on 367 individual seals [5] collected over three consecutive years (1998 to 2000). During this time, the total population was assumed to be ~1000 individuals. Therefore, the basis for the model has a very high sample size compared to the total population. Modelling the population structure, rather than using the age distribution of captured seals directly, was necessary since immature individuals were underrepresented in the dataset (grey circles in Figure 5). This underrepresentation was likely an effect of sampling taking place during the breeding period at active pupping sites, which are mainly occupied by adult individuals and pups of the year [3]. The estimated proportion of pups (0.25) produced by the model is

consistent with earlier observational data from Prins Karls Forland late in the pupping period (0.24) [21]. This figure is somewhat higher than what has been found in other harbour seal studies, where the proportion of pups ranges from 0.18 to 0.20 [47]. However, the remarkable absence of older individuals in the harbour seal population in Svalbard [5] is consistent with the finding of a higher proportion of younger individuals in the total population. Further, an estimated mortality rate of 0.21 for all age classes (except pups) is very similar to the estimated mortality rate (0.20) for all age classes in Pacific harbour seals (*P. v. richardii*) [48]. So the modelled stationary age structure appears to represent the age classes reasonably well. Since this population structure assumes a stable age composition, it should not be used to explore trend analyses for this population since changes in the age composition, a potential reason for shifts in the abundance of the population, would be masked [35,49,50].

Only the coastline of Prins Karls Forland was surveyed in this study because this area was believed to be the focal haul-out area for this species in Svalbard [1,3,36]. However, in the last few years an increasing number of harbour seals have been observed hauling out in other areas within the Svalbard Archipelago during the summer ([51,52], Norwegian Polar Institute Marine Mammal Sighting Database, <http://mms.data.npolar.no/accounts/>). Prins Karls Forland undoubtedly still represents the major breeding and moulting area for this species in this region, but due to the wider spread of this population it is reasonable to believe that the population of harbour seals could already be somewhat larger than the estimate herein.

Accurate assessments of a total population of harbour seals in Svalbard in the future will have to be based on aerial surveys during the moulting period that encompass a broader geographic spread that at least serially encompasses the full range of the species in the region. Additionally, it is clear that replicate surveys should be flown to minimise the impact of stochastic and other acute disturbances (e.g. polar bear predation). If correction factors from this study are to be applied to future surveys, these surveys should take place within the modelled time frame and temperature range documented in this investigation, as extrapolations outside the data range markedly increase the uncertainty of the estimates. Further, an attempt should be made to derive an approximate age structure for the population for each abundance estimate in order to detect possible shifts in age structure [35].

This study has shown that an estimated 1888 (CI: 1660-3023) harbour seals were found along the west coast of Prins Karls Forland, and that this number was likely quite stable from 2009 to 2010 (Table 3). However, despite the fact that (1) the surveys were performed at a high altitude to avoid frightening hauled out individuals; (2) the aerial digital stereoscopic photographic surveys were performed during optimal conditions to detect the largest possible proportion of the population hauled out; (3) an attempt was made to identify age structure shifts during the moult based on length measurements of seals from stereoscopic images; (4) the results from the digital images for two of the three surveys were reliable and of high quality; and (5) the estimate was adjusted for seals in the water at the time of the surveys, following the complex haul-out behaviour of different age and sex classes of harbour seals during the pupping and moulting season and corrected for the respective proportion in the total population, it is still likely that the estimate represents a modest underestimate of the real population size, because of the expanding distribution of this population within the Svalbard Archipelago.

This small population occupies a limited spatial range [1,3], is isolated from neighbouring harbour seal populations and demonstrates low genetic diversity [4], all of which make it vulnerable to stochastic mortality events. This means that it is at risk within the current scenario of climate change in the Arctic, particularly with respect to changing disease exposure [53]. However, for this northernmost population of harbour seals, a warming Arctic will likely have a positive impact since more suitable habitat will become available [54], and resident ice-associated seals that likely compete for food resources currently [55,56] are expected to experience population declines in the coming decades [57].

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Figures

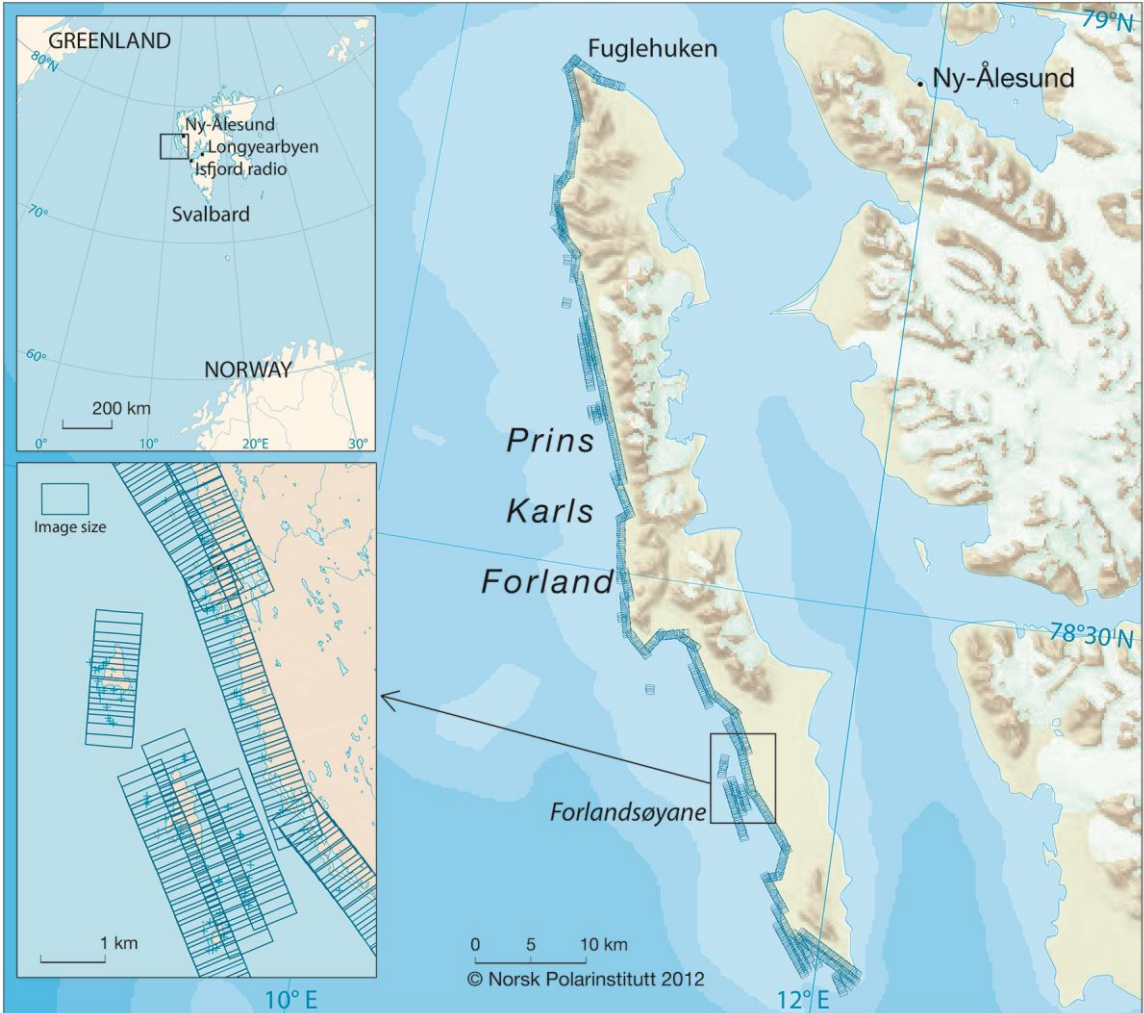


Figure 1. Map of Prins Karls Forland showing the extent of the aerial surveys flown and the locations Fuglehuken and Forlandsøyane. Top left panel shows the locations of Prins Karls Forland, Ny-Ålesund, Longyearbyen and Isfjord Radio within the Svalbard Archipelago. Bottom left panel shows Forlandsøyane and the adjacent coast as an example of the size and structure of the overlapping images taken along the whole west coast of Prins Karls Forland during each of the surveys.

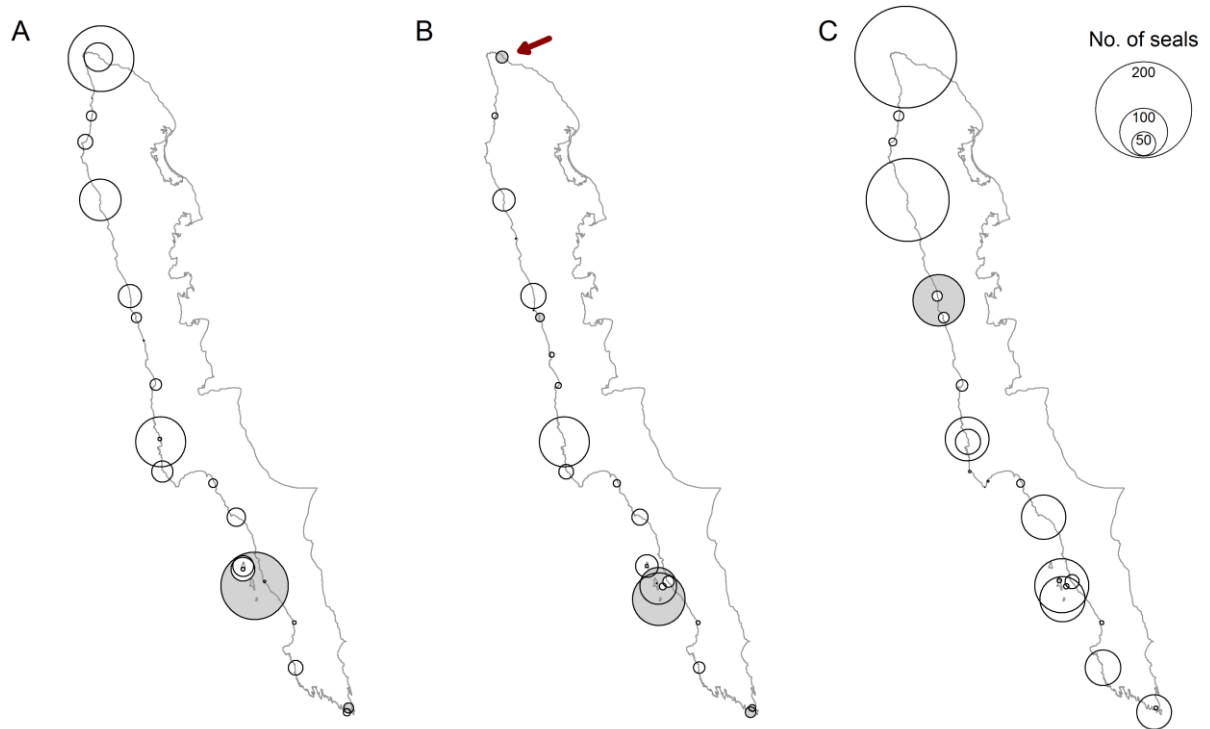


Figure 2. Distribution and group sizes of hauled out harbour seals along the west coast of Prins Karls Forland during three aerial surveys. Shaded circles indicate haul out areas that were disturbed i.e. some animals were moving towards the water. The red arrow indicates a hauled out site that was disturbed by a polar bear. A, B and C represent the survey results from 01 August 2009, 01 August 2010 and 19 August 2010, respectively.

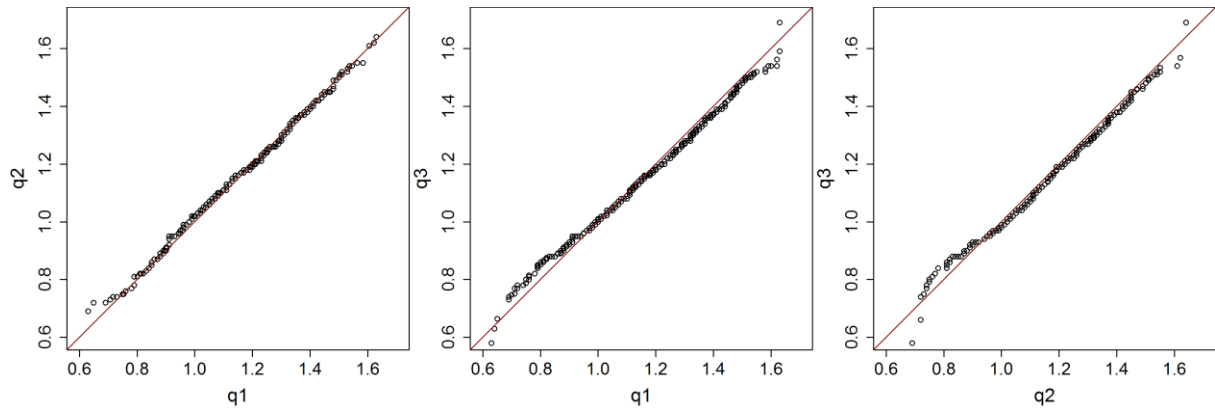


Figure 3. Quantile-Quantile plots, comparing the length distributions of the harbour seals in each of the three surveys against each other. q1, q2 and q3 represent the quantiles of the length distribution (m) for 01 August 2009 survey, 01 August 2010 survey and 19 August 2010 survey, respectively. The red line in each panel would indicate complete equality of the two distributions being compared.

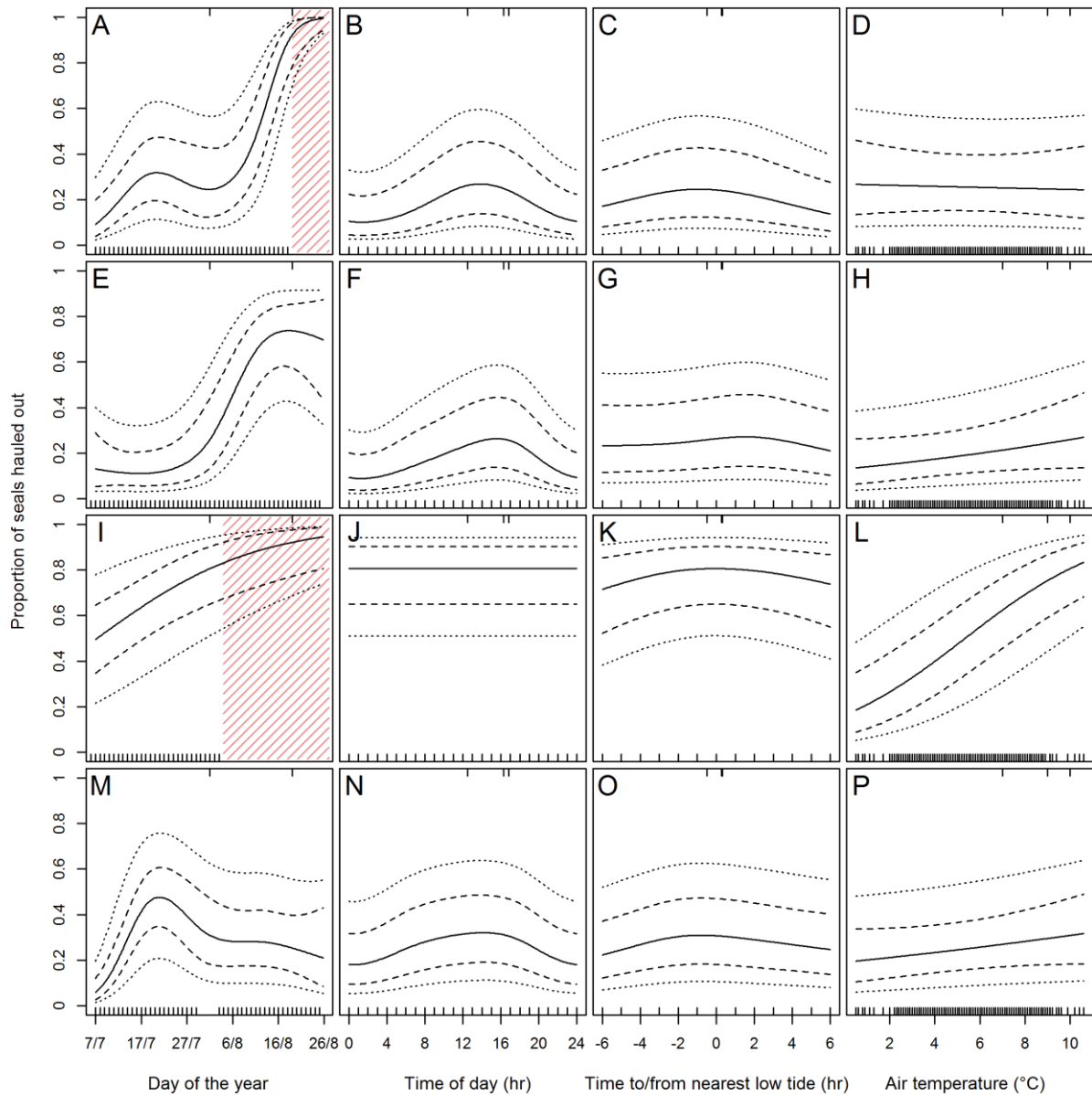


Figure 4. Fitted models of proportions of VHF-tagged seals hauled out depending on day of the year (panel A, E, I, M), time of day (B, F, J, N), hours to/from nearest low tide (C, G, K, O) and air temperature (D, H, L, P) for each of the four groups; adult females (A, B, C, D), adult males (E, F, G, H), juveniles (I, J, K, L) and pups (M, N, O, P). Each panel shows the fitted predictions (solid line) using the observed values for the 01 August 2009 aerial survey for the three other predictor variables for each group. The stippled lines represent 95 % CI (± 2 SE on a logit scale) around the means and the outermost dotted lines show the uncertainty in the predictions for a random individual seal (including both uncertainty in the means as well as the random between seal variation; *i.e.* $\pm 2(SE^2 + \delta^2)^{0.5}$). The distribution of the predictor variables is shown along the bottom of each panel, and the distribution of the variables related to each aerial survey is shown along the top of each panel. Shaded areas in panel A and I show extrapolations of the model, which are not based on real data.

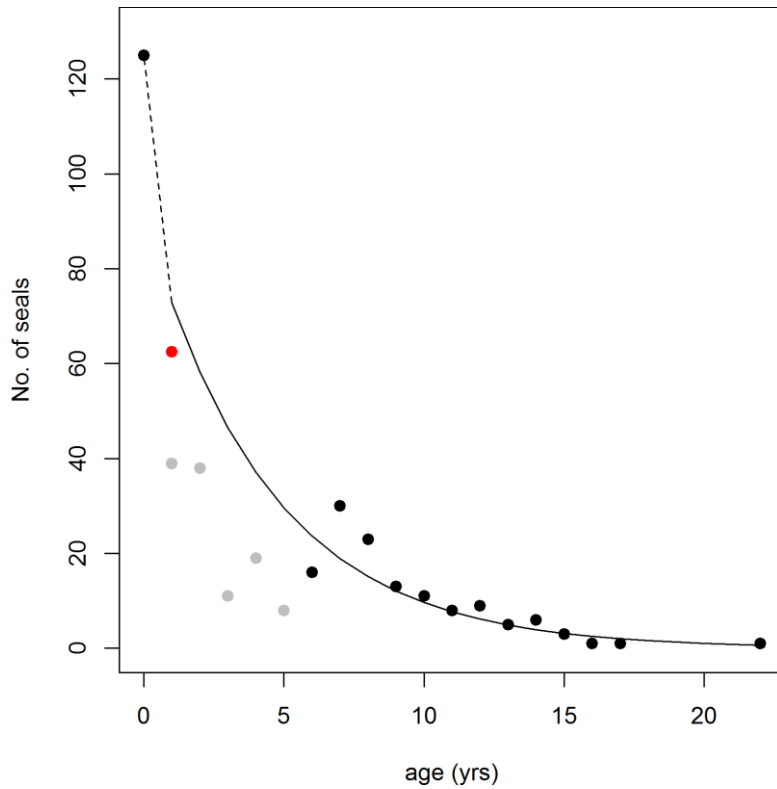


Figure 5. Number of seals caught versus their age in years (black and grey circles) [5]. The solid line shows the modeled age distribution. The stippled line shows a linear extrapolation from year class 0 to year class 1. The basis for this model is age class data (6-22 yrs - black circles), and an assumed 50 % pup mortality (red circle). Grey circles were excluded from the model because these age classes are assumed to be underrepresented in the capture data.

Tables

Table 1. Date (DOY, Day Of the Year), flight time (averaged for TIME), hours to/from nearest low tide (LOW TIDE), air temperature in °C (TEMP), number of seals counted on the digital aerial survey images in 2D and in stereo as well as the number of disturbed seals on images (for the three aerial surveys). LOW TIDE and TEMP are averaged values for each survey interval.

Survey No.	Date (DOY)	Time of day (TIME)	Hours to/from nearest low tide (LOW TIDE)	Air temperature (°C) (TEMP)	No. of seals counted on images in 2D	No. of seals counted on images in stereo (Y)	No. of disturbed seals on images in stereo
1	01.08.2009	15:36 - 18:06	-0.48	10	897	981	79
2	01.08.2010	11:14 - 13:43	0.32	7	782	730	252
3	19.08.2010	15:07 - 17:29	0.28	9	1245	1295	85

Table 2. ANOVA results with degrees of freedom (df), F value and p-values for each covariate and seal age/sex group (group). Day of the year (DOY), time of day (TIME) and hours to/from nearest low tide (LOW TIDE) are modelled as smooth functions. Therefore df, F values and p-values are approximations [58]. Significant values are in bold.

	Coefficient	df	F	p-value
Parametric	Air temperature (TEMP)	1.00	0.05	0.82
	group	3.00	9.60	< 0.0001
	TEMP * group	3.00	6.73	0.0002
Approximate	DOY adult females	3.54	23.81	< 0.0001
	DOY adult males	3.44	46.58	< 0.0001
	DOY juveniles	1.00	14.58	0.0001
	DOY pups	3.74	16.85	< 0.0001
	TIME adult females	2.50	14.67	< 0.0001
	TIME adult males	2.62	15.23	< 0.0001
	TIME juveniles	0.00	0.09	0.77
	TIME pups	2.47	9.82	< 0.0001
	LOW TIDE adult females	2.50	6.47	0.0007
	LOW TIDE adult males	2.36	1.08	0.34
	LOW TIDE juveniles	2.35	3.42	0.026
	LOW TIDE pups	2.47	3.76	0.017

Table 3. Estimated proportion of hauled out seals for each age/sex group for each survey, as well as the proportions of each seal group within the estimated stationary population age structure and the estimated total abundance of seals for each of the three aerial surveys based on stereoscopic images.

Survey No. (t)	Group (j)	Proportion of each group in the population ($q*100$)	Proportion of seals hauled out for each group ($p*100$)	Proportion of seals hauled out for each group in the population ($p*q*100$)	Correction factor (CI) ($1/\sum(p*q)$)	Population estimate (CI) (N)
1	adult females	15	24	4	1.92 (1.69-3.08)	1888 (1660-3023)
	adult males	15	26	4		
	juveniles	46	81	37		
	pups	25	31	8		
2	adult females	15	26	4	2.39 (1.89-4.86)	1742 (1381-3549)
	adult males	15	19	3		
	juveniles	46	62	29		
	pups	25	27	7		
3	adult females	15	92	14	1.40 (1.28-3.41)	1812 (1656-4418)
	adult males	15	73	11		
	juveniles	46	90	41		
	pups	25	24	6		