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Testing estimators of walrus abundance: insights from simulations of haul-out behaviour

T. Doniol-Valcroze, A. Mosnier and M.O. Hammill

Science Branch
Fisheries and Oceans Canada
Maurice-Lamontagne Institute
850 Route de la Mer
Mont-Joli, Quebec, G5H 3Z4

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Foreword

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

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ABSTRACT

Walrus are a challenging species to enumerate owing to their clumped distribution and the highly variable proportion of animals hauled out at any one time. Previous attempts to describe this variability using a statistical framework assuming a uniform or a binomial distribution underestimate the uncertainty in haul-out proportions. Based on simulations, we determined that a more appropriate approach is to consider that counts follow a beta-binomial distribution which takes into account the overdispersion due to correlation among hauled-out walruses. Using this framework, four abundance estimators were examined for bias in estimating the size of a simulated population, with the number of animals hauled-out following a beta-binomial distribution with known parameters. The Minimum Counted Population (MCP) and Bounded Count (BC) methods were both likely to underestimate the true population size, even when corrected by an estimate of the maximum proportion of the population that can be hauled-out at any given time. The Simple Count (SC) method, using mean counts corrected by the average proportion of time hauled-out, provides a reliable and unbiased estimator. Previous implementations of the MCP, BC and SC methods did not provide a realistic estimator of variance. Based on the beta-binomial framework, we propose a variance estimator for the SC method that takes into account the extra variance linked to the behavioural correlation among individual walrus. We also suggest a Bayesian estimator that provides a valid point estimate of the population size as well as a full and convenient description of the error distribution.

**Méthodes d’estimation de l’abondance des morses :
Leçons tirées de simulations du comportement sur les échoueries**

RÉSUMÉ

Le morse est une espèce difficile à dénombrer en raison de sa distribution agrégée et de la proportion très variable des animaux qu’on peut retrouver hors de l'eau. Les tentatives précédentes pour décrire cette variabilité à l'aide d'un cadre statistique supposant une distribution uniforme ou binomiale sous-estiment l'incertitude autour des proportions d’individus échoués. Grâce à des simulations, nous avons déterminé que l’utilisation d’une approche considérant que les comptes observés suivent une distribution bêta-binomiale, prenant en compte la variance supplémentaire causée par la corrélation entre les morses, est plus appropriée pour modéliser l'incertitude autour des proportions d'animaux échoués. En se basant sur ce cadre statistique, nous avons testé quatre estimateurs de la taille d'une population simulée, à partir de comptes d’animaux échoués tirés d'une distribution bêta-binomiale ayant des paramètres connus. Les méthodes de la Population Minimale Comptée (MCP) et du Compte Borné (BC) étaient toutes deux susceptibles de sous-estimer la taille réelle de la population, même quand elles étaient corrigées par une estimation de la proportion maximale de la population qui peut se retrouver échouée à tout moment. La méthode du Simple Compte (SC), qui utilise la moyenne des comptes corrigée par la proportion moyenne du temps passé hors de l’eau, fournit un estimateur fiable et sans biais. Les mises en œuvre précédentes des méthodes MCP, BC et SC ne fournissaient pas d’estimation réaliste de la variance. Nous proposons un estimateur de variance pour la méthode de SC qui prend en considération le cadre bêta-binomial et permet ainsi de tenir compte de la variance supplémentaire liée à la corrélation comportementale entre les morses. Nous proposons également un estimateur bayésien fournissant une estimation valide de la taille de la population ainsi qu'une description complète et pratique de la distribution de l'erreur.

INTRODUCTION

Walruses in Canada and Greenland are harvested for subsistence, in addition to a limited sports hunt in Canada. The Committee on Species of Endangered Wildlife in Canada (COSEWIC) has assessed Atlantic walrus as ‘Special Concern (COSEWIC 2006). Walrus are also listed under Appendix III of the Convention on International Trade in Endangered Species (CITES), which means that a permit from the Canadian CITES authorities is required to export walrus parts from Canada.

Walrus are a challenging species to enumerate. Two approaches are generally used to assess their abundance. One approach is to survey along parallel lines and record walrus sightings using line-transect or strip-transect methods. Such surveys are usually flown during the spring (April-May), when walrus may be hauled-out on the ice (eg Udevitz et al. 2001; Heide-Jørgensen et al. 2013). A second approach, involves coastal surveys, visiting haulout sites and floating ice in areas where walrus are known to occur during summer or early fall.

Bias during surveys arises from two main sources: not all animals are detected by observers or on photographs (detectability bias) and not all animals are available to be detected (availability bias). Each of these factors will also have its own variance. Using vertical photographs and multiple counts of these photographs, detectability bias can be considered to be quite low in walrus surveys (Mansfield and St Aubin 1991, Stewart et al. 2014b). However, several studies have identified that the proportion of the population hauled out at any one time may fluctuate considerably (e.g. Stewart et al. 2014a,b; Udevitz et al. 2009; Lydersen et al. 2008; Mansfield and St Aubin 1991). Mansfield and St Aubin (1991) flew repeated surveys of the same area to count walrus during July-August 1976 and 1977, and noted that daily counts varied from as few as 6 to as many as 2171 walruses hauled out (fig. 1, Appendix tables A1 and A2).

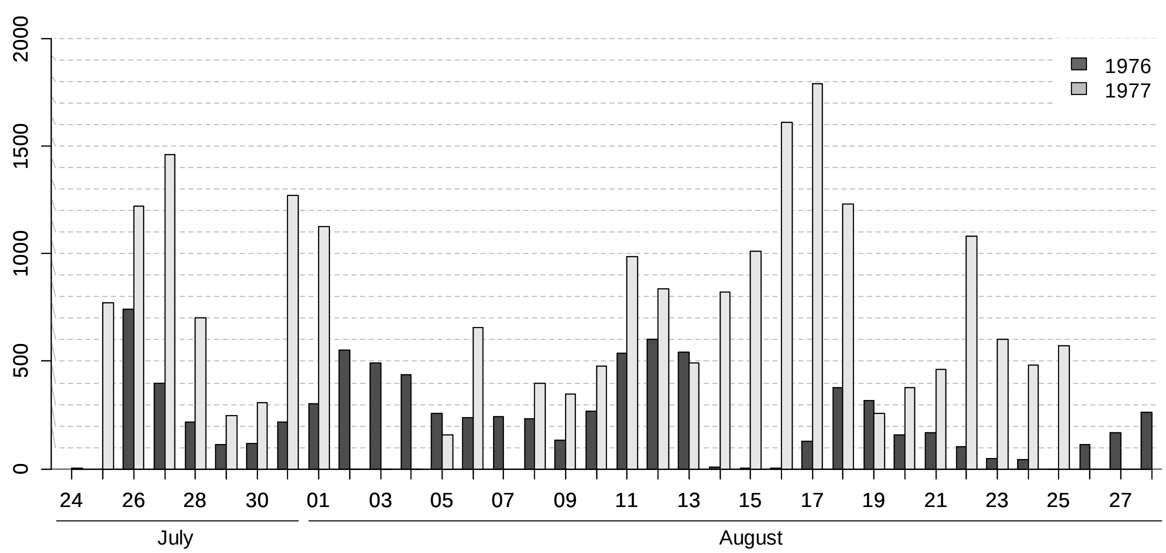

Figure 1. Maximum daily counts recorded at a haulout site on eastern Coats Island in 1976 and 1977 from Mansfield and St Aubin (1991).

Walrus surveys must often cover large areas, which by financial, logistical or temporal necessity limits the opportunities for repeated counts. This also leads to a challenge in interpretation of what a single count represents, and how this count or a series of haulout counts can be used to obtain a reasonable estimate of walrus abundance. The question can be broken into two components. The first component is to obtain a count of animals hauled out, while the second component involves a factor to adjust for the proportion of the population that is not hauled out when the counts were made.

Three types of counts have been used to estimate walrus abundance, either on their own, or in combination with some haulout correction factor. These counts can be referred to as Simple Counts (SC), Minimum Counted Population (MCP) and Bounded Counts (BC) (e.g., Johnson et al. 2007; Stewart et al. 2013, 2014 a,b). The SC are counts of hauled out animals. If a haulout site is visited more than once, then the mean of the counts for that site is taken. MCP are also counts of hauled out animals, and are identical to SC if haulout sites are visited only once. However, if a haulout site is visited more than once, then the highest count for that site is retained, and the lower counts are excluded from the analysis. In the case of BC, multiple visits are made to a haul out site or sites. The BC method assumes that each possible count is distributed uniformly, between 0 and the total number of individuals that haul out at that site. Thus it is assumed that the difference between the true number and a count is the same as the difference between the largest count, and the next largest count (Johnson et al. 2007).

Once a count of hauled out walrus has been obtained, it must be adjusted for the proportion of animals that were in the water at the time the haul-out was surveyed. One approach to obtain this information might be to use a series of regular (hourly or daily) counts (eg Mansfield and St Aubin 1991), but at best it would give an estimate of the maximum proportion hauled-out. More recently, satellite transmitters have been deployed, and counts have been corrected for animals in the water by using the telemetry data on numbers hauled out or time spent hauled out to develop an adjustment factor (eg Udevitz et al. 2009, Lydersen et al. 2008; Stewart et al. 2013, 2014a,b). However, the corrections have been applied in different ways by trying to model haulout behavior with respect to environmental conditions (Udevitz et al. 2009, Lydersen et al. 2008), by applying a correction based on the average proportion of animals hauled out, or by assuming that counts such as MCP and BC represent counts made under favourable conditions, which necessitates a different correction factor based on what is considered as more favourable haulout conditons (Stewart et al. 2014a,b).

In this study, we use two sets of simulations to gain insights into the performance of the different estimation methods. In the first part, we simulate the haul-out behavior of walrus to understand what causes the large variability in the proportion of walrus hauled-out and to determine the statistical distribution that underlies walrus count data. In the second part, we use this distribution to simulate walrus surveys of a theoretical population and test the efficiency of several estimators, including a Bayesian count model developed specifically to take into account the results of the first part.

MODELLING WALRUS HAUL-OUT BEHAVIOUR

To estimate abundance of walrus on haul-out sites, it is important to understand the impact of their hauling-out behaviour on the variability of counts made during surveys. Let us assume that each individual walrus spends a proportion P of its time hauled-out, and that this proportion is the same for all individuals in the population (e.g. because of physiological constraints). For each unit of time t (e.g., 1 hour), let us assume that whether a single walrus individual is hauled-out or not is the result of a Bernoulli draw with probability P, and that all individuals are independent of one another. We illustrate this by simulating the haul-out behaviour of 20 individual walrus that each spends 25% of their time hauled-out (fig. 2).

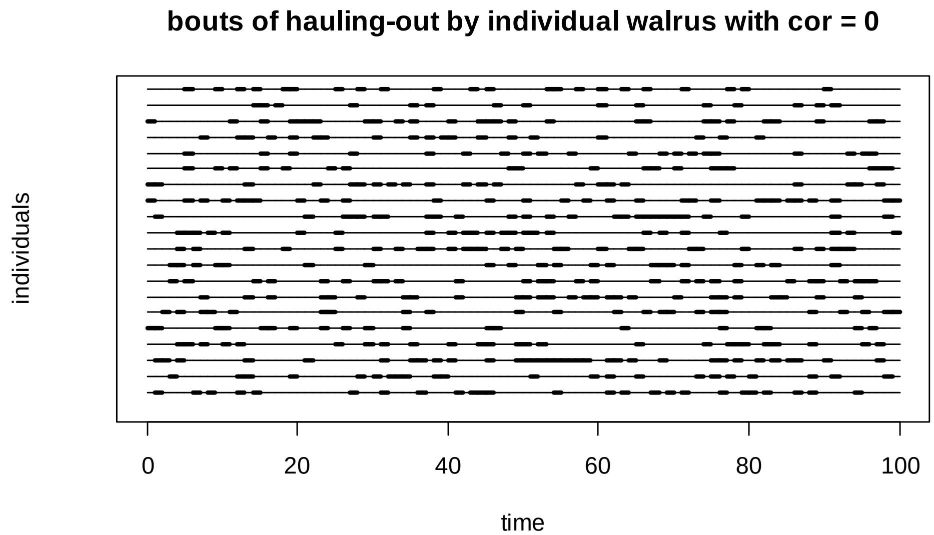

Figure 2. Haul-out behaviour of 20 simulated walrus over 100 hours. Haul-out bouts are represented as thick bold segments.

If we calculate the average time spent hauled-out for each walrus (i.e., counting time units spent hauled-out on the horizontal axis of fig. 2), the distribution follows closely the input value of *P* (fig. 3 left). Previous telemetry studies have mostly focused on estimating the average value of *P* as precisely as possible, but the low variability among individuals clearly cannot explain the large variability in observed counts, that are seen in studies such as those by Mansfield and St Aubin (1991)(fig. 1). Instead, what is of interest for survey counts is the proportion of walrus hauled-out at any given time (i.e., summing hauled-out individuals along the vertical axis for each time *t*). The resulting distribution is much more variable (fig. 3 right).

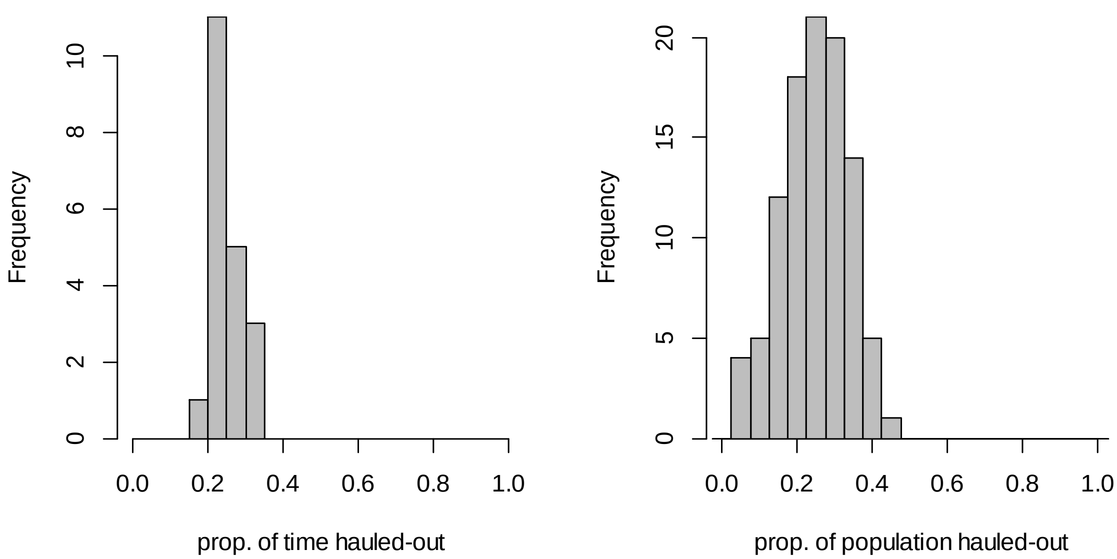

Figure 3. Haul-out behaviour of 20 simulated walrus over 100 hours. Left: average proportion of time spent hauled-out for each individual walrus. Right: proportion of the population hauled-out at any given time (over 100 hours).

For the entire population of *N* walrus, the number of walrus hauled-out *X* at any given time *t* follows a binomial distribution $X \sim Bin(N,P)$, which has mean NP and variance $NP(1-P)$.

Expressed as a proportion of the entire population, the mean is *P* with variance *P(1-P)/N*. For any large number of walrus, this variance will be very small. For instance, for a group of 100 walrus, the variance of repeated survey counts performed at different times above the haul-out site will be exceedingly small (fig. 4) and thus cannot account for the variability that is observed in real-life surveys (fig. 1).

The extra variance (overdispersion) could be due to heterogeneity in *P* among individuals in the population (e.g., sex, age classes, physiological state). However, there is little evidence of this in published studies (i.e., individual proportions are relatively similar and variance around mean *P* is small). This small variance cannot explain the discrepancies among counts and poorly quantifies the true uncertainty around our survey estimates. Overdispersion will also appear if the walrus individuals are not independent from one another in their hauling behaviour, either because of social structure or because different individuals seek out the same environmental conditions (e.g. Lydersen et al. 2008). Regardless of the reason, correlation among individuals results in higher variance than expected from a regular binomial distribution.

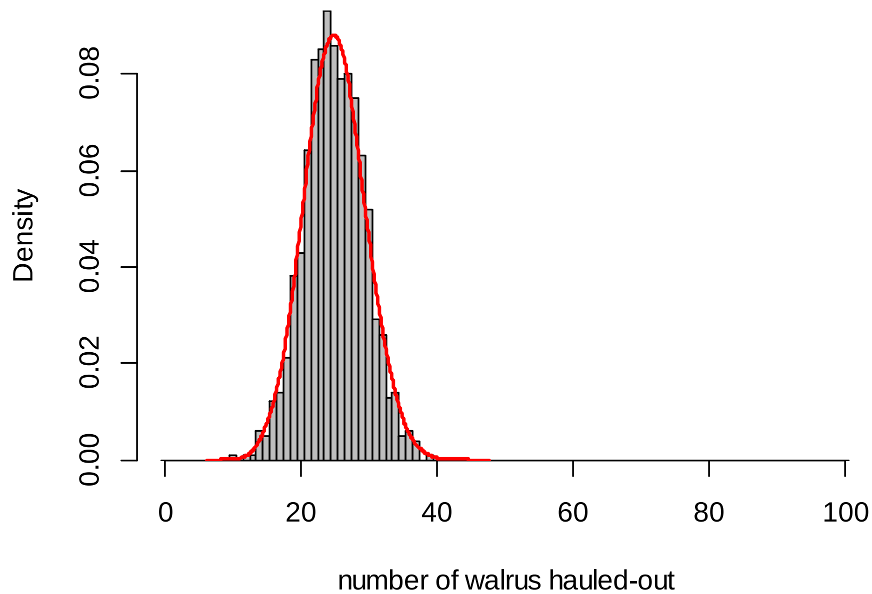

Figure 4. Number of walrus counted in surveys of a population of N=100 with P=0.25. Histogram: empirical distribution of counts of hauled-out walrus based on 100 simulated individuals over 1000 hours. Red line: probability density function of X ~ Bin(N,P).

The extra variance σ^2 due to the overdispersion is quantified as $\sigma^2 = 1 + (N-1)\rho$ with ρ being the mean correlation factor among individuals. If we simulate the same 20 walrus as before but we add a ρ =30% correlation among individuals, we see that different individuals align their hauled-out bouts more often (fig. 5 left) and the proportion of the population hauled-out at any given time becomes much more variable (fig. 5 right). In particular, the occurrences of time periods during which no walrus are hauled-out become more common. We note that the resulting pattern is similar to that observed in Svalbard and by Udevitz et al. (2009) in their telemetry studies (Appendix figures A1 and A2).

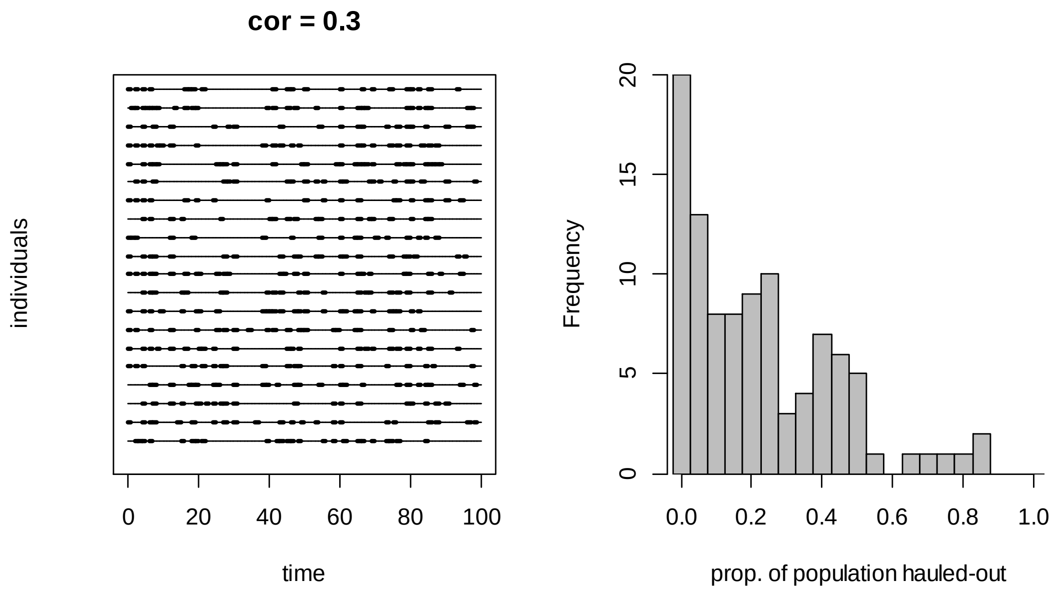

Figure 5. Left: Haul-out behaviour of 20 simulated walrus over 100 hours with 30% correlation among individuals. Haul-out bouts are represented as thick bold segments. Right: proportion of the population hauled-out at any given time (over 100 hours).

Such correlated Bernouilli trials can be modelled with a beta-binomial distribution (Skellam 1948). That is, X follows a binomial distribution $Bin(N,P)$ with P itself following a beta distribution $Beta(a, b)$ that can also be parametrized as a function of P and ρ the correlation factor. In other words, $X \sim BetaBin(N,P,\rho)$. This beta-binomial distribution reproduces empirical simulations (fig. 6) and proposes a much more realistic framework to explain the observations of the proportion of walrus hauled-out from telemetry studies and variability in survey counts.

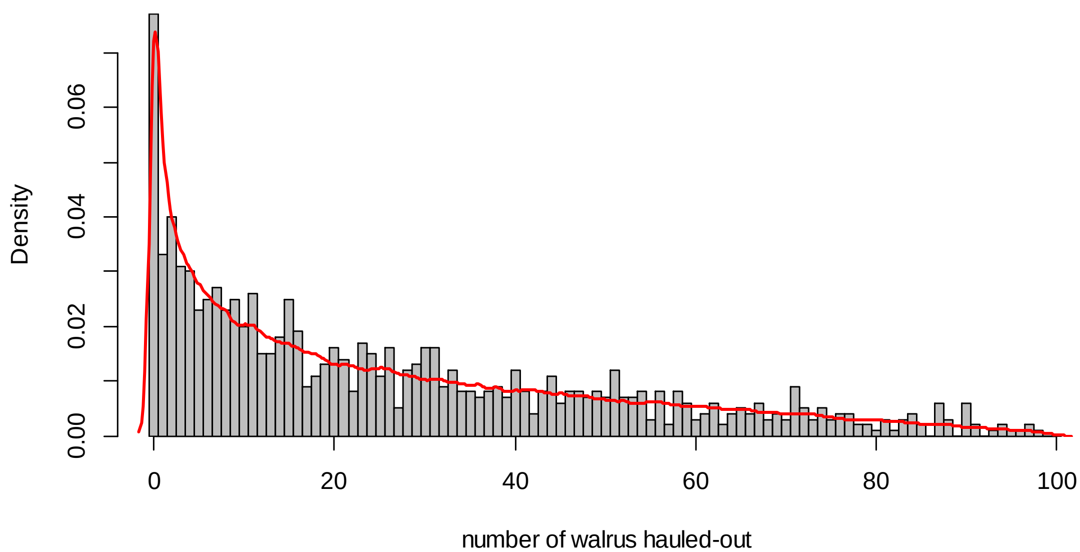

Figure 6. Number of walrus counted while hauled-out in simulated surveys of a population of N=100 with P=0.25 and ρ=0.3. Histogram: empirical distribution of counts of hauled-out walrus based on 100 simulated individuals over 1000 hours. Red line: probability density function of X ~ BetaBin(N,P, ρ).

Similarly, using this framework, we can replicate the results of published telemetry studies. For instance, if we use the parameters estimated in Udevitz et al. (2009), i.e., mean P=0.17 for 28 walrus observed over 320 hours, we find that for $\rho = 0.11$, we find a similar distribution to that observed in the study (figure 7 in Udevitz et al. 2009, appendix fig. A2). We also note that a direct relationship exists between the extra variance due to overdispersion and the parameters ρ and N. For instance, the extra variance factor of 2.02 calculated from raw telemetry data in Lydersen et al. for 28 walrus individuals corresponds to a correlation factor among walrus of $\rho = 0.04$. It is therefore clear that even a small correlation among individuals in haul-out behaviour can have a dramatic effect on the variability of the proportion of the population that is hauled-out at any given time, and thus on the variability of survey counts.

TESTING ABUNDANCE ESTIMATORS USING SIMULATED WALRUS COUNTS

Based on the examination of walrus haul-out behaviour above, we propose a framework for realistic simulations of walrus haul-out sites and of surveys taking place to estimate abundance at these sites.

First, we assume a haul-out site for which the true population size N = 1000 walrus. We assume that the mean proportion of time that walrus spend hauled-out is P = 0.30 and that the correlation factor among walrus is ρ = 0.10. Based on these parameters, the number of walrus available to be counted by an aerial survey at any given time t follows the beta-binomial distribution $X \sim BetaBin(N,P,\rho)$ shown on fig. 7, with mean 300 and a CV of 0.49.

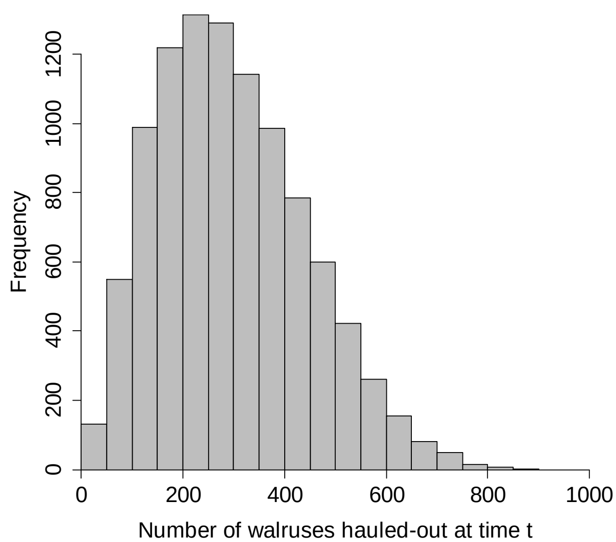

Figure 7. Number of walrus counted in surveys of a population of N=1000 with P=0.30 and rho=0.10.

We define P_{max}, the maximum proportion hauled-out at any given time, as the 99th percentile of this distribution, i.e. P_{max} = 0.68. We chose the 99th percentile because the actual maximum observed value is highly variable. Note that P_{max} is dependent on the sample size. For instance, if we simulate telemetry studies of 20 individuals, the 99th percentile is 0.75, a value similar to that reported in the literature for such small scale studies (fig. 8).

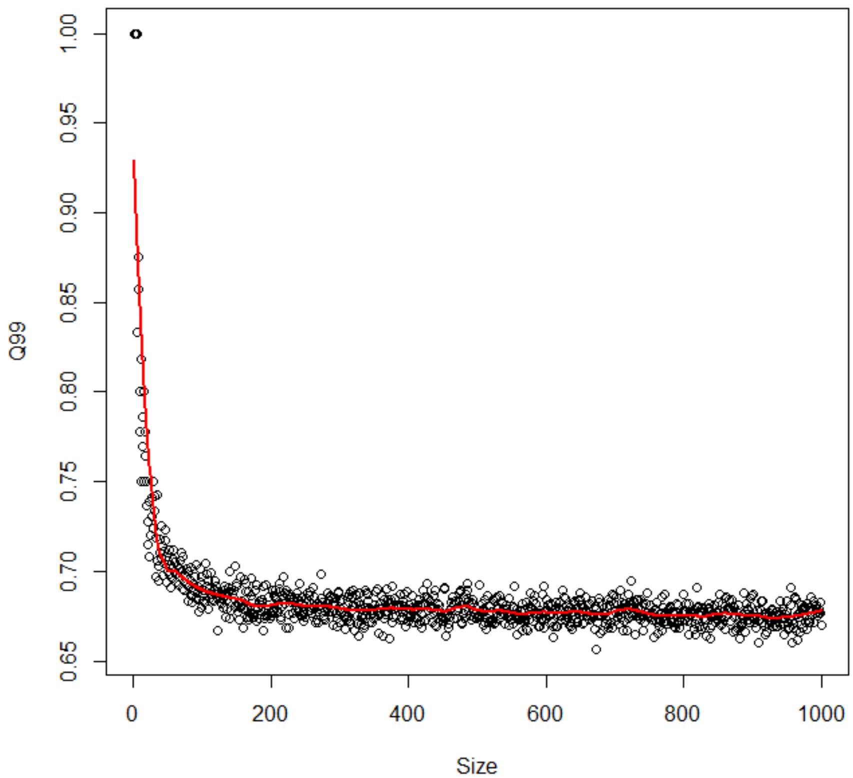

Figure 8. Value of the maximum proportion of walrus hauled-out at any given time, P_{max}, defined as the 99th percentile of the beta-binomial distribution BetaBin(N,P=0.30,$\rho = 0.10$), as a function of the population size N.

We use this beta-binomial distribution to simulate *k* counts C_1, C_2, …, C_k made by aerial surveys by drawing at random in this distribution. At this point, we assume that counts are made without error, i.e., that variance among counts stems entirely from the variability of the proportion hauled-out at any given time. We define C_{max} as the maximum observed count and C_{mean} as the mean of all counts. We estimate abundance using three approaches defined below.

MINIMUM COUNTED POPULATION (MCP)

A single count of hauled-out walrus at a specific site can only be equal or lower than the true population size. If the proportion of the population hauled-out at any given time is much lower than 1, then the count will have a strong downward bias. If several survey counts are available for the same site, the MCP (Stewart and Hamilton 2013; Stewart et al. 2014b) is based on the largest count for that site, C_{max}. Like a single count, C_{max} can only be equal or lower than the true population size. However, if there are enough surveys, the C_{max} will theoretically be closer to the true maximum number of walrus available for counting at any given time and will result in lower bias. Under the MCP approach, the estimated abundance is:

$$\widehat{N}_{MCP} = \frac{C_{max}}{P_{max}}$$

BOUNDED COUNT (BC)

The Bounded Count method assumes that *k* possible count values are distributed uniformly between 0 and the total number of individuals in the population (N) (Robson and Whitlock 1964; Johnson et al. 2007). Within this distribution, *k* random deviates are drawn, which divide the range of values into *k*+1 segments, whose expected values are identical. Thus, the difference between N and C_{max} is expected to be the same as the difference between C_{max} and C_{max-1}. Numerically, the bounded-count estimator is simply twice the largest count minus the second-largest count. Thus, the bounded count attempts to correct the downward bias of the minimum count and will provide a reliable estimate of N if several assumptions are met: P_{max} is close to 1, there are enough surveys (but see Routledge 1982), the probability of obtaining a count between 0 and N is uniform. If P_{max} is not close to 1 but is known (or can be estimated), then the Bounded Count can be corrected in the same way as the MCP. Note that if there is only one survey, the Bounded Count is identical to the MCP.

$$\widehat{N}_{BC} = \frac{2C_{max} - C_{max-1}}{P_{max}}$$

SIMPLE COUNT (SC)

The mean of several survey counts will always be lower than N. However, if it is then corrected by a reliable estimate of *P* (not P_{max}), then it will result in an unbiased estimate of N. Thus, the estimator is:

$$\widehat{N}_{SC} = \frac{C_{mean}}{P}$$

Note that in some cases, when there are few surveys and *P* is relatively large, it is possible for the corrected mean count to be lower than the highest of the counts. In that case, the estimator is replaced by the MCP.

BAYESIAN MODEL (BM)

In addition to estimators used in previous studies, we propose a simple Bayesian model of walrus counts based on the insights gained from our simulation of hauled-out behaviour. The model assumes that the observed counts follow a binomial distribution, for which the parameter P_t itself follows a beta distribution:

$$C_k \sim Bin(N, P_t)$$

$$P_t \sim Beta(a, b)$$

The hyper-parameters a and b are calculated so that the resulting beta-binomial distribution has mean *P* and correlation ρ (presumed known):

$$a = (\frac{1}{\rho} - 1)/(1 + \frac{1-P}{P})$$

$$b = a \times \frac{1-P}{P}$$

A uninformative prior is given to N to let it range between 0 and a maximum (in this case we chose N_{max} = 5,000):

$$N = N_{max} \times \omega$$

$$\omega \sim Beta(0.025,1)$$

Parameter *N* was estimated by updating the prior to a posterior distribution based on the count data, using a MCMC approach in JAGS (Plummer 2003). Posterior distributions were examined in the R programming language (R Core Team 2015), using packages R2jags and coda (Plummer et al. 2006, Su and Yajima 2015). After a burn-in of 10,000 samples, every 5th point was kept from 5 chains of 10,000 iterations, for a total of 10,000 samples.

SIMULATION RESULTS

We ran 1000 simulation, each representing 3 surveys of a single site, and computed the four estimators. At this point, we assumed that P and P_{max} are known with certainty. We then compared the distribution of the estimates to the true value of N (fig. 9).

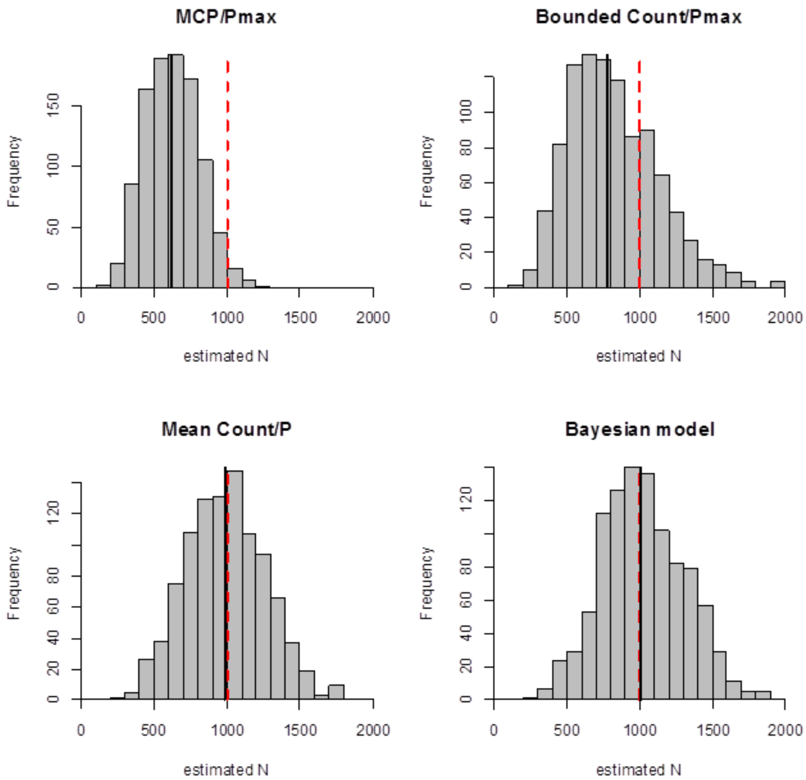

Figure 9. Estimators of abundance based on 1000 simulated surveys. In each survey, 3 counts are made in a population of 1000 walrus with P = 0.30 and ρ = 0.10. Black line: median of estimates. Red dashed line: true population size.

Results show that both the MCP and BC methods underestimated the population size, even when they were corrected by the real value of P_{max} (i.e., the value of P_{max} from the distribution that produced the simulated observations). The BC was closer to the true N than the MCP but had a longer right tail.

In contrast, both the SC and the BM resulted in point estimates that were centered on the true population size, with a more symmetrical distribution around N than the MCP and BC. With few surveys, the two estimators can produce estimates that are far above or below the real N. However, when increasing the number of surveys, they converge rapidly towards the correct estimate (fig. 10).

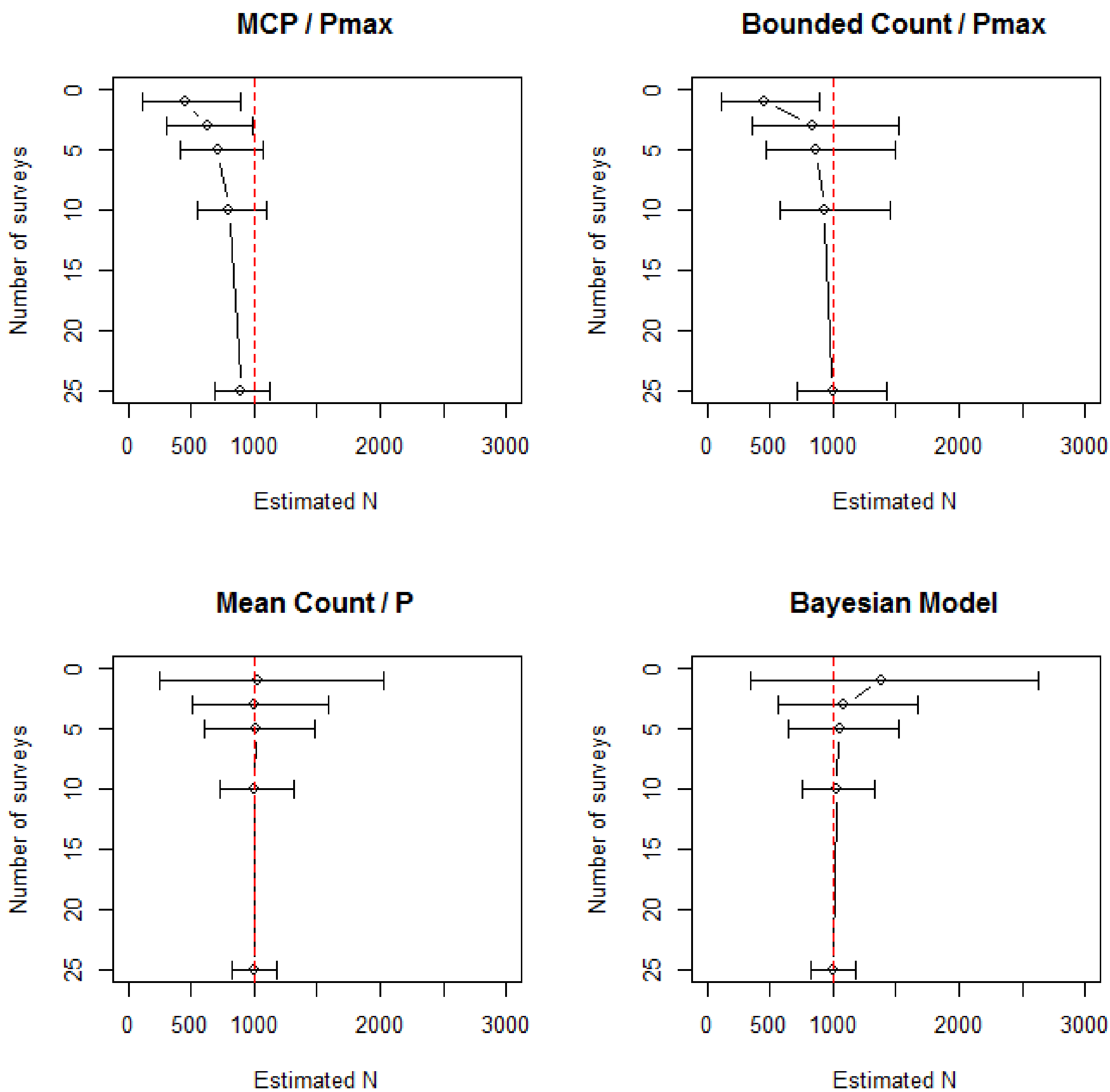

Figure 10. Estimators of abundance with increasing numbers of surveys (1, 3, 5, 10 and 25). Each run is based on 1000 simulated surveys, in which counts are made in a population of 1000 walrus with P = 0.30 and ρ = 0.10. Open circle: mean of estimates. Horizontal intervals contain 95% of simulation results. Red dashed line: true population size.

ESTIMATION OF VARIANCE

Estimating uncertainty around the point estimate is crucial for risk-based management. The MCP approach has no estimator of variance *per se* (although variance around the estimate of P_{max} could be used to estimate part of the uncertainty). Similarly, the BC approach has no straightforward estimator of variance but a $(1-\propto) \times 100\%$ confidence interval is usually computed with the lower limit $N_L = C_{max}$ and the upper limit $N_U = C_{max} + (C_{max} - C_{max-1}) \times (1-\propto)/\propto$. If BC is corrected for P_{max}, then the upper confidence limit should also be divided by

P_{max}. From there, a crude standard error can be back-calculated by assuming for instance a lognormal error distribution.

In previous walrus studies (e.g., Steward et al. 2014b), a formula for the variance of the corrected bounded count or average count was taken from Thompson and Seber (1994):

$$var(Count_{corr}) = \frac{var(Count)}{P^2} + Count_{corr}\frac{1-P}{P} + \frac{Count_{corr}^2}{P^2}var(P)$$

This formula was designed for the variance of an estimator with imperfect detectability, with multiple sites being surveyed once. The first term reflects variance among sample sites (for instance, in a Simple Random Sampling design). The middle term reflects variance in counts due to imperfect detectability (from a binomial distribution). The last term is added to incorporate uncertainty in the estimated value of the mean haul-out proportion. Essentially, this formula considers that the variance in counts and the variance due to the imperfect detection are two independent sources of variability. Moreover, it does not take into account the variability of *P* that is responsible for the overdispersion. Therefore, we suggest that the formula is not appropriate for multiple counts of walrus on the same study site, with most of the variability in counts driven by the variability in availability.

Here, we suggest a formula for the SC that takes into account the beta-binomial model. If $\widehat{N} = C_{mean}/P$ and $C_{mean} = \frac{1}{k}\sum_1^{i=k} C_i$ with *k* the number of counts, then:

$$var(\widehat{N}) = \frac{var(C_{mean})}{P^2} = \frac{var(\sum_1^{i=k} C_i)}{k^2P^2} = \frac{k\ var(C)}{k^2P^2} = \frac{var(C)}{k\ P^2}$$

In the beta-binomial framework, $var(C) = \widehat{N} \times P \times (1-P) \times \sigma^2$ with σ^2 the over-dispersion factor. Thus:

$$var(\widehat{N}) = \widehat{N}\frac{1-P}{k\ P} \times \sigma^2$$

where σ^2 is expressed by its relation with the correlation factor ρ as $\sigma^2 = 1 + (\widehat{N} - 1)\rho$. The standard error of the estimator is the square root of $var(\widehat{N})$. To compute a Confidence Interval, we suggest assuming a lognormal distribution around $\widehat{N}$. In the rare cases where the lower confidence bound is less than the highest of the counts, the lower bound is replaced by that highest count value.

In the case of the Bayesian estimator, the standard error of the estimator is simply the standard deviation of the posterior distribution of the estimated population size. The quantiles of the posterior distribution can be used directly to compute Credible Intervals. The CI bounds of the Bayesian estimator can never be inferior to the highest count and thus require no correction.

For example, if the three survey counts are { 367, 155, 292 }, the estimates are $\widehat{N}_{MCP} = 540$, $\widehat{N}_{BC} = 650$, $\widehat{N}_{SC} = 904$, and $\widehat{N}_{BM} = 964$. The estimated variance for the simple count is:

$$var(\widehat{N}_{SC}) = 904 \times \frac{1-0.3}{3 \times 0.3} \times [1 + (904-1) \times 0.10]$$

And $SE(\widehat{N}_{SC}) = \sqrt{var(\widehat{N}_{SC})} = 253.4$ (CV 28%). For comparison, the SE around the Bayesian estimator ($\widehat{N}_{BM}$) is 298.5 (CV 31%).

UNCERTAINTY AROUND THE VALUE *P*

So far, we have considered that availability P_t varies in time but that the mean value of P in the population is known without error. We now develop the framework further to include uncertainty around the value of the haul-out proportion, which becomes a random variable with a normally-distributed error (*SD_P*) around its point estimate $\hat{P}$. We assume that $var(\hat{P}) = SD_P{}^2$ is estimated from an independent study (e.g., telemetry).

With uncertainty around P, the Simple Count estimator of abundance becomes $\hat{N}_{SC} = C_{mean}/\hat{P}$, which does not change its point estimate. To calculate its variance, we follow Thompson and Seber (1994) and use the delta-method approximation. The full variance becomes:

$$var(\hat{N}) \cong \hat{N}\frac{1-P}{k\,P} \times \sigma^2 \; + \frac{\hat{N}^2}{P^2} var(P)$$

Note that the first term will decrease with an increasing number of surveys whereas the variance due to uncertainty around P will not.

For the Bayesian model, we replace the fixed value of P in the calculation of Beta coefficients a and b with $P \sim N(\hat{P}, SD_P)$, i.e., P becomes a hyper-parameter of P_t.

To take into account the uncertainty around P in the calculation of the corrected Bounded Count estimator, one must recalculate the value of P_{max}. (For instance, if $N = 1000, \hat{P} = 0.30$, $\rho = 0.10$, and $SD_P = 0.015$, then $P_{max} = 0.70$.).

COVERAGE PROBABILITIES

To validate the methods and estimate the reliability of the confidence intervals around the estimators, we ran 10,000 simulations with counts made in a population of 1000 walrus with $\hat{P} = 0.30$, $\rho = 0.10$ and $SD_P = 0.015$ (equivalent to a CV of around $\hat{P}$ of 5%). We tested the effect of an increasing number of surveys (1, 3, 5, 10 and 25). In each case, we counted how many times the true value of the population size was included in the 95% CI. Table 1 shows that when there are few surveys, the coverage of the SC methods is slightly lower than the nominal value of 95%, whereas the BM approach maintains a better coverage. As pointed out by Routledge (1982) in a similar analysis, the coverage probability of the BC estimator is always inferior to 95% over the range of values tested.

Table 1. Coverage probabilities of the 95% CI for each estimator. Each run is based on 10,000 simulated surveys, in which counts are made in a population of 1000 walrus with P = 0.30, ρ = 0.10 and $SD_P = 0.01$. The MCP does not provide an estimator of variance and thus no confidence interval can be calculated.

Number of surveys	1	3	5	10	25
SC	89.2%	93.3%	93.9%	94.0%	95.0%
BM	95.9%	94.6%	94.6%	95.5%	94.8%
BC	-	90.4%	91.0%	91.1%	92.9%

DISCUSSION

Biases due to imperfect detectability or incomplete availability are a problem in numerous wildlife studies, and various techniques have been proposed to account or correct for missed animals. Walrus counts made repeatedly on the same haul-out site typically show considerable variability. Previous statistical frameworks (i.e. assuming that counts are the results of a uniform distribution, or a binomial distribution based on the mean haul-out proportion in the population) could not explain this variability. In this document, we have started by simulating individual haul-out behaviour of walrus and showing that the resulting distribution of population-level counts can adequately be modelled by a beta-binomial distribution.

Using both empirical individual-level simulations and the corresponding beta-binomial distribution, we have shown that introducing even a low amount of correlation among individuals (e.g., 5-10%) results in considerable variability in the proportion of the population hauled-out at any given time. This is the result of more synchronous behaviour among individual walrus, which increases the probabilities that either very few (even zero) or a large proportion of the population can be hauled-out at the same time. This framework allows us to reproduce and explain the results observed in both telemetry studies and survey counts.

Previous studies have focused mostly on estimating the mean proportion of time that walrus spend haul-out, in order to use it as a correction factor for survey counts. This proportion seems to vary relatively little among individuals, which could be the result of physiological constraints, and therefore has little variance. Moreover, previous modelling efforts have used the error about the estimate of this proportion as the source of uncertainty in their estimates of population size. In effect, the more precisely this proportion was known, the less uncertainty in the abundance estimate. We suggest that this approach is flawed because it cannot account for the large variability observed in counts and does not model the error distribution appropriately. We have shown that it is more realistic to take into account the variability in the proportion of the population hauled-out at any given time.

The beta-binomial framework has several implications for abundance estimates. First, it explains why counts are so variable even when conducted at short intervals and shows that any single count of walrus haul-out sites should be treated with great caution. Indeed, even with a small amount of inter-individual correlation, it is quite possible – even likely – for a count to be representative of 5%, 25% or 60% of the population. Even when correcting with an estimate of the mean haul-out proportion, a single count can result in a serious under- or over-estimate. Multiple surveys of the same haul-out sites at short intervals within the same year will therefore provide more useful information than single surveys performed in multiple years.

Several estimators of abundance use either the mean P or P_{max} to correct for unavailable walrus. This proposed framework suggests that the mean P is a valid correction factor. For methods that rely on P_{max}, we propose a method to calculate P_{max} based on the assumed correlation factor. Indeed, if P_{max} is estimated from telemetry studies based on a few individuals (e.g., 0.74), it is incorrect to use the same value when correcting for a presumably much larger population. We examined this using simulations and found that P_{max} decreases quickly with increasing sample size, but stabilizes beyond 50 individuals (with a P_{max} ~0.68 when P=0.30 and $\rho = 0.10$). Since most sites will presumably have at least that many walrus, using this approximation for P_{max} should improve estimates for MCP and BC.

This framework also allowed us to simulate sites to be counted and to test the validity and precision of four estimators of abundance. Our results showed that even with a correct estimate of P_{max}, the estimators MCP and BC tend to severely underestimate the true population size, presumably because their basic assumptions are not met. Our results show that a simple mean of the counts yields a reliable and unbiased point estimate, even with a low number of surveys. With this in mind, we have proposed a different estimator of variance for the simple count that takes into account the extra variance that originates from the overdispersion of the underlying beta-binomial distribution. This overdispersion is linked directly to the correlation coefficient among individual walrus via a simple numerical equation. This means that a telemetry study aiming at estimating this correlation can be used directly to inform the error distribution of abundance estimates. This simple estimator performs well, although our simulations suggest that its coverage may be slightly insufficient when there are few surveys (less than 3).

We have also proposed a Bayesian estimator developed on the assumption of a beta-binomial distribution of counts. This method provides a valid point estimate as well as a full and convenient description of the error distribution, with adequate coverage probability, thus removing the need to assume a log-normal error distribution when calculating the CV or N_{min} for PBR or population modelling. Another potential advantage of the Bayesian approach is that it could be integrated directly into a larger Bayesian model of population dynamics.

In our first step, we have assumed that the true value of *P* was known without error. Obviously, if the value of *P* used in the calculations is incorrect, the estimate could be strongly biased. We have thus expanded the simple count and Bayesian frameworks to include uncertainty around the mean value of *P* in the population (which is not the same as saying that P_t varies through time around its mean value; that part is handled by the beta-binomial overdispersion). Our simulations suggest that the added variance of the MCC estimator (approximated using the delta-method) may be slightly underestimated.

Theoretically, with enough surveys, the bounded count approach could provide a valid estimate of abundance without the need for an estimate of *P*, although if the true P_{max} is far below one, there will always a downward bias. However, simulations have shown that the uncorrected BC approach requires a large number of counts to provide a valid estimate, especially when *P* is low. We note that in theory, with a large number of sites and surveys, *P* and the even correlation factor ρ could be estimated from the count data under the Bayesian approach.

In view of our simulations, our advice is that analyses of walrus surveys take into account the beta-binomial statistical framework that underlies the resulting counts, by using the corrected simple count with the appropriate variance estimator or the Bayesian count model. Based on comparisons with published telemetry studies and the variability observed in walrus count studies in general, we are suggesting that correlations factors of 5%–15% be used until more information becomes available.

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APPENDIX

Table A1. Walrus counts in the Southampton-Coats Island area of Hudson Bay during July-August 1976-77. [1] Counts from 3 haulout sites on Coats Island. (Mansfield and St Aubin 1991).

Date	Walrus Island	Bencas Island	Cape Préfontaine	Cape Pembroke	East[1] Coats	Sea Ice	Total
1976-07-24	297[a]	167[a]	0	240[a]	536[a]	-	1230
1976-07-24	169[a]	0	0	0	561[a]	-	730
1976-07-25	368[a]	0	33[a]	0	1090[a]	-	1491
1976-07-26	103[a]	0	102[a]	30	992[a]	-	1227
1976-07-27	250	0	92[a]	282[a]	773[a]	-	1397
1976-07-28	75	0	103[a]	345[a]	333[a]	-	856
1976-07-29	15	15	12	30	175	-	232
1976-07-30	8	0	75	0	175	-	258
1976-07-31	9	0	20	0	225	-	254
1976-08-01	7	0	195	0	450	-	652
1976-08-03	0	0	160[a]	50	536[a]	-	746
1976-08-04	0	0	7	12	750	-	769
1977-07-20	0	-	0	0	20	6	26
1977-07-21	0	-	-	-	-	800	800
1977-07-22	0	-	-	-	0	300	300
1977-07-23	25	-	-	-	-	675	700
1977-07-24	0	-	0	0	6	-	6
1977-07-26	0	-	25	0	1721[a]	425	2171
1977-07-26	-	-	-	-	-	625	625
1977-07-28	0	-	0	13	125	0	138
1977-07-29	0	-	0	248[a]	179[a]	0	427
1977-08-01	0	-	70	150	1113[a]	0	1333

[a] Estimates based in the mean of triplicate counts from photographs

Table A2. Maximum daily counts from one haulout site located at 62° 46' N, 81° 56' Won eastern Coats Island during July-August, 1976-77 estimated from Figure 2 of Mansfield and St Aubin (1991).

Date	1976	1977
24-juil	-	1
25-juil	-	770
26-juil	740	1220
27-juil	400	1460
28-juil	220	700
29-juil	115	250
30-juil	120	310
31-juil	220	1270
01-août	305	1125
02-août	550	0
03-août	490	0
04-août	440	0
05-août	260	160
06-août	240	655
07-août	245	-
08-août	235	400
09-août	135	350
10-août	270	475
11-août	535	985
12-août	600	835
13-août	540	490
14-août	10	820
15-août	5	1010
16-août	3	1610
17-août	130	1790
18-août	380	1230
19-août	320	260
20-août	160	380
21-août	170	460
22-août	105	1080
23-août	50	600
24-août	45	480
25-août	0	570
26-août	115	-
27-août	170	-
28-août	265	-

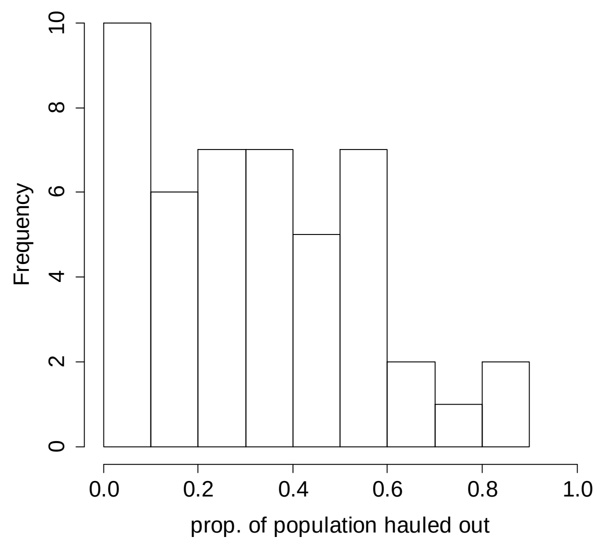

Figure A1. Proportion of 11 tagged walrus hauled out on any single day. Based on data from figure 3 in Lydersen et al (2008). In figure 5 of this document, we take into account overdispersion due to correlation among walrus when estimating the variance in haulout behaviour. The resulting distribution compares more favourably with observed haulout behaviour from Svalbard.

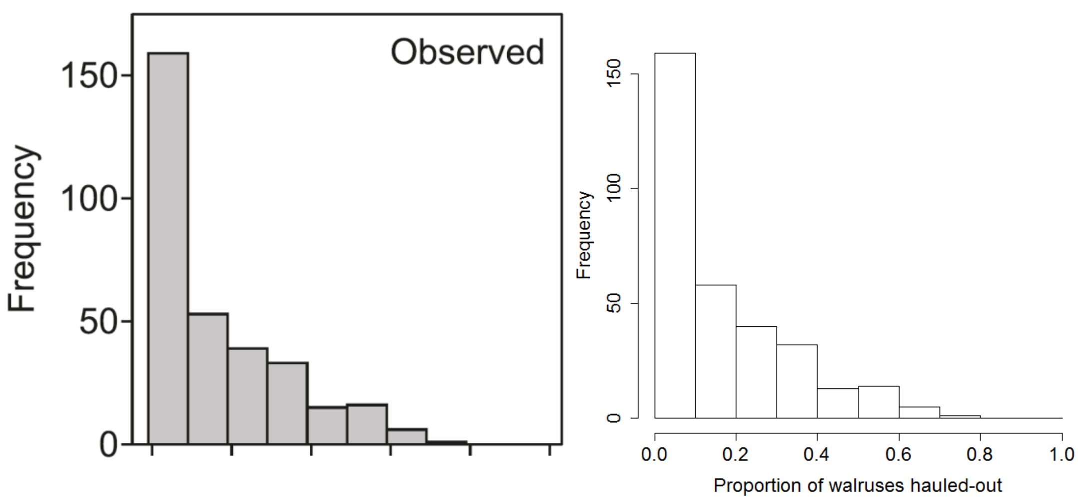

Figure A2. Left: Frequency histogram of observed proportion of tagged walruses (N = 10) hauled-out at 322 behavioral intervals, from figure 7 in Udevitz et al. (2009). Right: Frequency histogram of proportion hauled-out walruses from a simulated population using 332 samples from beta-binomial distribution with parameters N = 10, P = 0.17 and ρ = 0.11.