Information is gained increasingly fast in capture-recapture surveys - bowheads assessed by photographic surveys, and minke whales by genetic marking?

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Abstract

The expected Fisher information gain per extra capture in a sequential capture-recapture experiment is found to grow faster than linear in number of captures when the population is closed and homogeneous. A similar pattern is found for open populations, with information gain growing faster to its maximum the shorter the longevity is. From simulating photographic capture-recapture surveys off Barrow in the spring, from 2008 and with effort as in previous such surveys, the abundance estimate for the BCB bowhead population based on photo-ID data is found to be about 9% in 2022. The Fisher information in an abundance estimate based on mark-recapture data is calculated for an imagined program of biopsy sampling. If each year 50 northeastern Atlantic minke whales are biopsy sampled, and 600 are taken in the catch, the cv of the abundance estimate will be some 12% after 25 years of the program.

1 Introduction

Abundance estimates for whale populations are usually obtained from direct count methods. These could be visual line transect surveys by ship or aeroplane, or they might be visual surveys from a static point on the migratory route. The abundance of the Bering-Chukchi-Beaufort Seas population of bowhead whales (the BCB bowhead *Balaena mysticetus*) is estimated from visual spring surveys combined with acoustic data from a fixed station at the ice close to Barrow. Earlier, when tags could be recovered from sufficient numbers of

harvested whale, mark-recapture data provided useful information on absolute abundance and trends.

For small and well-marked populations, photographic capture-recapture studies are widely used for abundance estimation. The proposition of this paper is that regular photographic surveys might in the long run provide sufficient data for abundance estimation for long-lived cetaceans such as the BCB bowhead, even though the BCB bowhead is relatively abundant (around 10 000 individuals) and many of the individuals have very weak natural markings. We do this by proving that the information gain per unit survey effort increases nearly linearly in the accumulated amount of survey effort. This is proved for a closed and homogeneous population. With surveys of the same size in years $t = 1, 2, \cdots$, the cv of the captur-recapture abundance estimate after t surveys is of the order $1/t$, while t direct counting surveys would yield an estimate with cv of the order $1/\sqrt{t}$. This is at least the case for t small to moderate, say less than 30 years for the long-lived bowhead. Although long-lived, the BCB bowhead constitutes an open population. To get some insight into the Fisher information in an imagined continued capture-recapture surveys of the BCB bowhead, a program of biopsy sampling is considered. With 10 biopsies sampled and with genotyping of 60 harvested bowheads each year, the gain in Fisher information in the abundance estimator based on these accumulated data only, is found to increase concavely towards a stationary level after some 300 years, and reach half of its maximal level after 35 years. For the first 30 years the information gain curves slightly, but increases basically linearly during these years of "investment" in the marking archive. This makes the cv of the abundance estimate based on such a biopsy sampling only to be of the order $1/t$ for $t \leq 30$ years of the program

Photographic surveys of cetaceans, and also biopsy sampling and identification by genotype, are cases of sequential capture-recapture experiments called Schnabel census after Schnabel (1938). Individuals are captured one by one and recorded with respect to identity. As the cumulated number of captures increases, whether a new capture turns out to be a recapture or not seems intuitively to be increasingly more informative since it is seen on an ever more informative background. This is proved to be the case for a closed homogeneous population. The favorable rate of information gain found in the simple theoretical model might hold up even for open populations. This is actually born out in our simple theoretical study of biopsy sampling. It is further demonstrated by simulating continued photographic surveys of the BCB bowhead. Individuals are assumed to have natural marks of varying degree, and are captured according the model and parameter estimates of Schweder et al. (2009).

Dependent on the survey costs for the visual surveys, biopsy sampling and photographic surveying, an optimal mix of these three types of surveys could be worked out. If the criterion is to minimize the cv of the combined abundance estimator after t years for given total cost, there might be a crossing point $\widetilde{t}$ such that for $t > \widetilde{t}$ the abundance estimate from the photographic surveys combined with the capture-recapture data from biopsies has a smaller cv than the abundance estimate from direct surveys combined over the t years. The reason is that the 1/cv based on capture-recapture data will grow convexly,

while that from direct surveys will grow linearly in t. Biopsy sampling and photographic surveys would however also yield data of value for other aspects of the biology of the BCB population of bowhead whales.

Northern minke whales cannot be made subject to photographic surveys since they have few natural marks that are visible in the short glimpse when they surface. They are however uniquely marked by their genotype. An imagined program of biopsy sampling is considered. Each year m individuals are genotyped by biopsy in the field, and all harvested whales are also genotyped. The likelihood of the recapture data obtained from t years of such a program is approximated by a product of conditionally independent Poisson components, and the Fisher information is calculated. For parameters plausible for the northeastern Atlantic minke whale, 25 years of biopsy sampling would yield an abundance estimate with coefficient of variation 12.2% under the assumption of constant population, natural mortality independent of age, and random sampling in the catch and the biopsy marking. In addition to information on abundance, a program of biopsy sampling would indeed yield information on natural mortality, migration and other aspects of the biology of minke whales.

2 Closed homogeneous populations

Statistical theory has developed considerably since Petersen (1896) first marked m plaice, and later on sampled n individuals of which M were marked. He estimated the abundance by mn/M (Seber 1982; Borchers, Buckland, and Zucchini 2002; Chao 2001).

Yip (1991) studied the Schnabel census for a closed population of size N by martingale methods. He found that a new observation optimally should have weight proportional to $1/(N-m)$ where m is the number of unique captures or marked individuals so far. A related result is obtained in the following using classical methods of analysis.

Consider the simplest possible Schnabel census with one individual randomly sampled from a homogeneous closed population of size N at each sampling occasion $n = 1, \cdots$. The population is closed in the sense that no individuals are lost from the population by death or migration, and their is no recruitment to the population. It is homogeneous in that all individuals have the same probability $1/N$ to be the next capture, independently of the previous captures.

The sampled individual is either a recapture or a new capture. A recapture links up with one of the observed capture histories, while a new capture starts a new capture history. With m capture histories, the the next capture might be regarded as a multinomial experiment with $m+1$ possible outcomes. Outcome $i \leq m$ is that the capture is a recapture of individual i in the observed set. The last outcome is that the capture is of an individual not previously captured, starting capture history $m+1$. The probabilities for each of these first m outcomes are all $\frac{1}{N}$, while the capture is new with probability $\frac{N-m}{N}$.

Let H_n be the observed set of capture histories obtained from the n first captures, and let $L_n(N) = P_N(H_n)$ be the likelihood of the m observed cap-

ture histories in H_n. The sharper curved this likelihood is at the top, the more informative is the maximum likelihood estimator. Disregarding that the parameter to be estimated, N, is a natural number, the Fisher information of L_n is defined (Pawitan 2001) as

$$I_n = E\left[-\frac{d^2}{dN^2}\log L_n\right].$$

Since

$$L_{n+1} = L_n \cdot P\left(H_{n+1}|H_n\right) = L_n \cdot \left(\frac{1}{N}\right)^{Y_{n+1}}\left(\frac{N-m}{N}\right)^{1-Y_{n+1}}$$

where Y_{n+1} is the Bernoulli distributed indicator for capture number $n+1$ being a recapture. The information gain is consequently

$$\begin{aligned} I_{n+1} - I_n &= E\left[\left(-\frac{d^2}{d\theta^2}\log P\left(H_{n+1}|H_n\right)\right)|H_n\right] \\ &= \frac{m}{N}\left[-\frac{d^2}{dN^2}\left(\log\frac{1}{N}\right)\right] + \frac{N-m}{N}\left[-\frac{d^2}{dN^2}\left(\log\frac{N-m}{N}\right)\right] \\ &= \frac{1}{N^2}\frac{m}{N-m}. \end{aligned}$$

The m capture histories are equally likely when the capture is a recapture. We could therefore also argue that the likelihood gain of the next capture is that of a Bernoulli experiment with odds $m/\left(N-m\right)$. The variance of the score for this experiment, with Y indicating that the capture is a recapture, is also

$$Ig = var\left(\frac{d}{dN}\left(Y\log\frac{m}{N} + (1-Y)\log\frac{N-m}{N}\right)\right) = \frac{1}{N^2}\frac{m}{N-m}$$

as long as $m < N$. This is also the conditional Fisher information gain, and it is the innovation variance in the score process, which is a martingale.

A third approach is to visit the process each time a new unique capture is made. Let $R_k \geq 0$ be the number of recaptures from new capture number k to new capture number $k+1$, and let m be the number of unique captures, $n = m + R_1 + \cdots + R_{m-1} + W$ where $W \geq 0$ is the length of the final run of recaptures. The number of recaptures is $n-m$. The runs of recaptures are independent and geometrically distributed, $P\left(R_k = r\right) = \frac{N-k}{N}\left(\frac{k}{N}\right)^r \quad r = 0, 1, \cdots$. The log likelihood is thus

$$l\left(N\right) = \sum_{k=1}^{m-1}\left[R_k \ln\left(\frac{k}{N}\right) + \ln\left(\frac{N-k}{N}\right)\right] + W\ln\left(\frac{m}{N}\right). \tag{1}$$

Assume now that sampling is stopped when the mth new capture is made, $m \leq N$, i.e. $W = 0$. The score function and Fisher information (Pawitan 2001)

is respectively

$$
\begin{aligned}
S_m &= \frac{dl}{dN} = \frac{1}{N}\sum_{k=1}^{m-1}\left[\frac{k}{N-k} - R_k\right], \\
I_m &= -E\frac{d^2 l}{dN^2} = \frac{1}{N}\sum_{k=1}^{m-1}\frac{k}{(N-k)^2}.
\end{aligned}
$$

The expected amount of field effort needed to continue until $m+1$ unique individuals are sampled is $1 + ER_m = \frac{N}{N-m}$.The expected information gain per expected unit of field effort is thus

$$
Ig = \frac{I_{m+1} - I_m}{ER_m} = \frac{1}{N^2}\frac{m}{N-m}, \tag{2}
$$

which is the Fisher information gain per capture.

By direct calculation $ES_m = 0$, and $varS_m = I_m$. These are standard results in regular statistical models (Pawitan 2001). The maximum likelihood estimator $\widehat{N}_m$ is the unique solution of $S_m(N) = 0$, and since the distribution of $S_m(N)/\sqrt{I_m}$ is close to the standard normal distribution when $m \leq N$ is large, $\sqrt{I_m}\left(\widehat{N}_m - N\right)$ is approximately standard normally distributed. Only in asymptotic schemes where both m and N tends to infinity is it possible to state precise asymptotic normality.

When $n \to \infty$ all individuals will sooner or later be sampled, this occurs after an expected number of captures approximately $N\ln(N)$. From then on $m = N$ and there will only be recaptures. From (1) we have with certainty that $\widehat{N} \to N$ as $n \to \infty$.

3 Photographic surveys of bowhead whales

Aerial photographs of BCB bowheads have been collected systematically during the spring migration near Point Barrow in many years during the past two decades (Angliss et al., 1995; Koski et al., 2006; Rugh, Koski and George, 2007). Previous statistical analyses of the database resulting from the aerial photo surveys demonstrated that these data are valuable for estimating abundance and demographic parameters for the population of bowhead whales (Rugh, 1990; da Silva et al., 2000; Zeh et al., 2002; Schweder, 2003; Schweder et al., 2009). In the present study the objective is to learn how information for key parameters (abundance, growth rate and mortality intensity) develops as more aerial photo surveys are conducted.

Captures are made in continuous time one by one, and the images from each capture are compared to those from previous captures to determine whether the capture is a recapture or not. Matching is done in the lab after the survey of the year. The population of bowhead whales is open to mortality and recruitments over the years of survey. Individuals might vary with respect to capture intensity, and they vary with respect to degree of visible marking.

We use the model of Schweder et al. (2009) and its fit to the photographic survey data consisting of yearly hours on effort, number of captures and number of recaptures in 10 years of survey between 1984 and 2003, for simulating the population process and the process of photographic surveying. The data are briefly summarized by a total of 4936 captures and 42 recaptures. The protocol for matching is designed to prevent false positive matches (Angliss et al. 1995).

The population is assumed to grow according to a deterministic lumped Pella Tomlinson model. Individuals are removed at a constant mortality rate. Each capture is characterized by degree of marking and quality of image for each of four dorsal regions. The probability of recognizing a true recapture as a recapture is modeled as a logistic regression in these eight variables. The capture intensity was assumed to vary randomly over the years and across individuals. Schweder et al. (2009) developed the likelihood function for data obtained from photographic surveying of this open and heterogeneous population. The likelihood function would be nearly correct if there were no false negative matches (true but unmatched recaptures), which there certainly are. The maximum likelihood estimates were corrected for bias by bootstrapping. The results of Schweder et al. (2009) is briefly that there hardly is individual variation in capture intensity. The capture intensity varies however over the years. The distribution of the matching probabilities turn out to be highly skewed towards low probabilities (Figure 1). This reflects that bowhead whales tend to be weakly and variably marked, but is also due to the very stringent protocol for matching.

We use a simplified version of this model in our present simulation study. The capture intensity is now assumed equal across years and individuals, and the population is assumed to grow exponentially. The parameter values are chosen to be consistent with the results of Schweder et al. (2009), but with a slightly increased mortality rate to speed up the population dynamics a bit. Yearly surveys with 71.4 hours at effort (the historical mean) are simulated from 2008 to 2022. The covariates for the logistic matching probability is for each simulated individual drawn from the corresponding observed distribution, and whether true recaptures are recognized and recorded as recaptures are simulated by corresponding Bernoulli draws. The parameters of the simplified model are estimated by maximizing the corresponding likelihood function based on the simulated data, in the same way as the more complex model was fitted to the observed data, but bootstrapping to correct for bias is not performed. We present results from 20 replicate simulations over the years 2003 - 2022. The observed data from 1984 to 2003 are used together with simulated data in all estimation. The year 2003 is special since captures had not been matched to captures from previous surveys. The simulation for 2003 does therefore only involve matchings to previous captures.

The simulation model was parametrized as shown in Table 1, together with 9 estimated parameters characterizing the probability of a true recapture being recognized as such and correctly matched. Each estimation involved thus 13 parameters. It was carried out by AD model builder (Otter research 2004). Standard errors are estimated from the Hessian matrix of the log likelihood function, and coefficients of variation are calculated by standard error divided by

estimated value. The mean (over replicates) cumulative number of respectively captures and recaptures increase from 5730 and 60 to 18952 and 325 over the simulation period 2008 to 2022.

The results are shown in Table 2 and Figure 2. They support the notion that information is gained faster in capture-recapture studies than by methods such as visual surveys where each unit of field effort contribute the same expected amount of information. Instead of standard errors and coefficient of variation dropping by the square rot of effort, our impression is that the rate of convergence rather is of the order $effort^{-1.04}$. That the marginal utility of a unit of field effort is increasing at this rate accords with our analysis of the simple Schnabel census. It is partly due to the photographic surveys indeed being surveys providing relative abundances from the capture rates. It also helps that the bowhead whale is long-lived.

The abundance of the Bering-Chukchi-Beaufort Seas population of bowhead whales has been estimated from ice-based visual and acoustic surveys at Point Barrow during the spring migration (Zeh and Punt 2005). This, and other more direct count methods, have constant information gain per unit field effort. At some level of field effort we should therefore expect abundance estimates from photographic surveys to out-compete the linear method, and from then on at an increasing margin. In assessments of this population there is no tradition for using abundance estimates from photographic surveys (Brandon and Wade 2006), although other results such as estimates of mortality (Zeh et al. 2002) are used. Our results, as well as those of Schweder et al (2009) partly presented in Table 1, give support for continued investment in photographic surveys of the bowhead whales off Alaska since these whales are subject to aboriginal subsistence hunt and must be assessed on a regular basis (International Whaling Commission 2003).

4 Biopsy sampling of minke whales?

It is the extreme longevity in bowhead whales that make the information gain of an additional round of capturing to grow about linearly over a prolonged period. Other whales, such as the minke whales, have higher mortality and the higher turn-over makes the information gain in an additional capture-recapture survey to curve faster towards an asymptote. This will be demonstrated for an imagined mark-recapture study for an ideal population resembling the northeastern Atlantic minke whale. The population is assumed to have large constant abundance, with recruitment balancing natural mortality and removals by yearly harvest of constant size.

The abundance of minke whales in the northeastern Atlantic is currently estimated by direct count methods, e.g. shipborn line transect surveys (Skaug et al. 2004). Every year one part of the total area is covered by a survey, and these partial surveys are integrated to estimate the abundance of the northeastern Atlantic stock of minke whales. Earlier, discovery marks were used. Some of these pieces of steel with a number on were recovered in harvested whales.

Beddington et al (1984) analyzed the data obtained from discovery marking of 333 minke whales around Bear Island in the Barents Sea over the years 1974 to 1978, of which 26 were recovered in the catches between 1975 and 1982. The catches varied in size from 1393 to 1860 whales over these years. Beddington et al (1984) found that abundance estimates from these data are rather sensitive to assumptions about the relative age distributions of marked and captured animals. Their abundance estimates have cv around 25%, and are in broad agreement with current understanding of minke whale abundance in the area. Recently nearly 600 minke whales are taken yearly in the Norwegian harvest. This is about 0.6% of the current stock. Every harvested whale is genotyped. A program of biopsy sampling and genotyping would provide data valuable both for estimating longevity in minke whales, their migratory pattern and their abundance.

The northern minke whale is not suitable for photographic studies, and it is only through some form of active marking that recaptures can be obtained. Let the imagined study be one of yearly biopsy sampling. For the northeastern atlantic minke whale a program of biopsy sampling should not be less feasible than a program of discovery-marking, and there will be no problem of tag loss since the every captured whale is genotyped.

The population is of constant but unknown size N. A program of biopsy sampling is stated in year $t = 0$. Each year m individuals are genetically marked immediately after the catch. The catch is assumed instantaneous, with only natural mortality acting between consecutive catch seasons. Marking and harvesting are assumed to be independent, and to be cases of simple random sampling. Let the yearly catch be of constant size C.

Let X_t be the number of previously marked individuals found in the catch and among the biopsy sampled in year t. The size of this combined sample is $C + m$. Let further $m - u_{st}$ be the number of individuals that where marked in year s, and that have been removed in years previous to t. There are thus u_{st} individuals in that marking cohort that might be sampled in year t. Some of these might however have died from natural causes. The probability of surviving from marking and until sampling in year t is S^{t-s} where $S = 1-M$ is the natural survival probability. The number of recaptures X_t is a sum of contributions from each of the previous marking cohorts. Let X_{st} be the number of recaptures from marking cohort s. Conditional on u_{st} X_{st} has mean $(C + m)\, u_{st} S^{t-s}/N$. Conditional on the results in previous years, the expected number of recaptures is

$$EX_t = \frac{C+m}{N} \sum_{s=0}^{t-1} u_{st} S^{t-s} = \frac{v_t}{N}.$$

Since abundance N is assumed large relative to the sampling $C + m$ the number of recaptures is approximately conditionally on v_t Poisson distributed. Using this as the likelihood contribution from the sampling result in year t, the conditional log likelihood gain is

$$l_t - l_{t-1} = X_t \log\left(\frac{v_t}{N}\right) - \frac{v_t}{N},$$

and $l_1 = X_1 \log\left(\frac{v_1}{N}\right) - \frac{v_1}{N}$ with $v_1 = (C+m)\,mS$. The gain in Fisher information is

$$\begin{aligned} E\left[-\frac{d^2}{dN^2}\left(l_t - l_{t-1}\right)\right] &= N^{-3} E E\left[\left[2v_t - NX_t\right]|v_t\right] \\ &= N^{-3} E v_t. \end{aligned}$$

The factor

$$v_t = (C+m)\sum_{s=0}^{t-1} u_{st} S^{t-s}$$

is stochastically increasing, and must have a mean increasing in t. To find this mean consider the expected number of removals by catch over the years $s+1, \cdots, t-1$. For $s=0$ and $t=2$ the removals are taken in year 1. To be caught the whale must survive until year 1, and then be caught. The probability for this is SF where F is the fishing mortality C/N. There are m individuals exposed to this event, and the expected number of removals is $E\left(m - u_{0,2}\right) = mSF$. In year $t=3$ there might be removals from those marked in year 0 and in year 1. A whale marked in year 0 can either be caught in year 1 or year 2. The probability of the union of these events is $mSF + mS\left(1-F\right)SF$. The expected number forms actually a geometric series, and

$$\begin{aligned} E\left(m - u_{st}\right) &= mSF \sum_{i=0}^{t-s-2} \left[S\left(1-F\right)\right]^i \\ &= mSF \frac{1 - \left[S\left(1-F\right)\right]^{t-s-1}}{1 - \left[S\left(1-F\right)\right]}, \end{aligned}$$

This yields

$$Ev_t = (C+m)\,m \sum_{s=0}^{t-1} \left[1 - SF \frac{1 - \left[S\left(1-F\right)\right]^{t-s-1}}{1 - \left[S\left(1-F\right)\right]}\right] S^{t-s}.$$

Summing up, the Fisher information gain from recaptures in the combined sample and catch in year t is

$$E\left[-\frac{d^2}{dN^2}\left(l_t - l_{t-1}\right)\right] = N^{-3}\left(C+m\right) m \sum_{s=0}^{t-1} \left[1 - SF \frac{1 - \left[S\left(1-F\right)\right]^{t-s-1}}{1 - \left[S\left(1-F\right)\right]}\right] S^{t-s}.$$

The Fisher information obtained from the recaptures in all the years $1, \cdots, t$ when m individuals are marked in each of the years $0, \cdots, t$ is the sum of these gains. Since the Fisher information of $\widehat{N}$ is an estimate of $1/var\left(\widehat{N}\right)$ the coefficient of variation of an abundance estimate based on these data will thus

approximately be

$$
\begin{aligned}
cv &= \frac{1}{\sqrt{E\left[-\frac{d^2}{dN^2} l_t\right]}} \frac{1}{N} \\
&= \sqrt{\frac{N}{(C+m)\, m \sum_{s=0}^{t-1} \left[1 - SF \frac{1-[S(1-F)]^{t-s-1}}{1-S(1-F)}\right] S^{t-s}}}.
\end{aligned}
$$

For the northeastern atlantic minke whale, realistic parameter values are $N = 100000$, $M = 0.044$, $S = 1 - M = 0.956$ and $C = 600$. The Fisher information gain grows nearly linearly for small t, but levels concavely off at an asymptote. It reaches half of its maximal value after 14 years for these parameter values. For $m = 50$ markings each year the cv of the abundance estimate is about 11.9% after 25 years of marking. The cv of the maximum likelihood estimate abundance based on these cumulative data is plotted against year in Figure (3) for various values of m.

A combination of line transect surveying and biopsy sampling might be an option for the monitoring of the northeastern Atlantic minke whale. Line transecting would indeed be necessary in the early years of a program of yearly biopsy sampling. Together with information on abundance, biopsy sampling would yield important information on other aspects of minke whale biology.

A similar biopsy sampling program is also considered for the long-lived BCB bowead, with natural mortality assumed to be 0.017 (Schweder et al. 2009). A harvest of 60 whales which all are genotyped, and 10 biopsies taken each year would make the information gain for each new survey to increase concavely towards a stationary level after some 200 years, and reach half of its maximal level after 35 years. For the first 30 years the information gain curves slightly, but increases basically linearly during these years of "investment" in the marking archive. This makes the cv of the nabundance estimate based on such a biopsy sampling only to be of the order $1/t$ for $t \leq 30$ years of the program, while direct surveying of effort proportional to t would have a cv proportional to $1/\sqrt{t}$.

In figure (4) the information gain in continued biopsy sampling and genotyped catch, relative to its maximum,.is ploted for the relatively shortlived minke whale and the long-lived bowhead whale.

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	Value	Estimate	95% CI
Abundance 1984	5500	4011	(2001, 9298)
Yearly growth rate	2.5%	3.2%	(1.0%, 8.4%)
Yearly mortality rate	2.2%	1.7%	(1.3%, 2.4%)
Hourly capture intensity	0.001	0.0015	(0.0008, 0.0027)

Table 1. Parameter values used in the simulation (Value). Estimates and 95% confidence intervals from Schweder at al. (2009)

year	cv	year	cv	year	cv	year	cv
2003	32	2011	23	2015	19	2019	13
2008	26	2012	26	2016	19	2020	13
2009	25	2013	22	2017	16	2021	11
2010	24	2014	22	2018	14	2022	9

Table 2. Estimated coefficient of variation (%) for abundance estimates based on sequentially cumulated data. The 2003 survey lasted 146.6 hours. 20 replicates of surveys in 2003, of length 146.6, and in 2008-2022, each of length 71.4 hours are simulated.

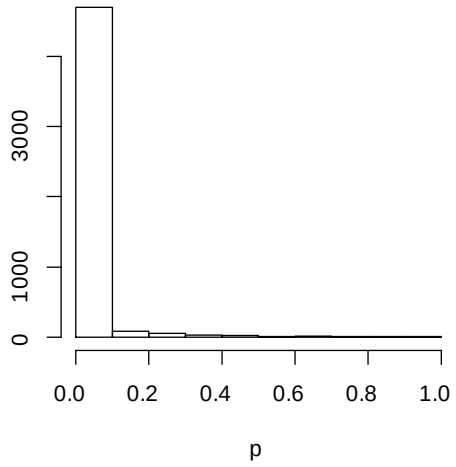

Figure 1: Histogram of estimated matching probabilities for individual captures (Schweder et al. 2009).

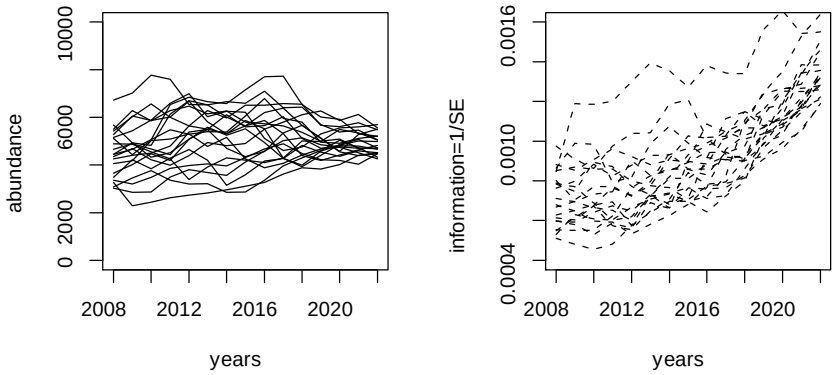

Figure 2: Estimated abundance of bowhead whales in year 1984 from surveys up to a given year (left), and information as measured by inverse standard error for abundance in 1984 based on surveys up to a given year (right). Simulated data, 20 replicates.

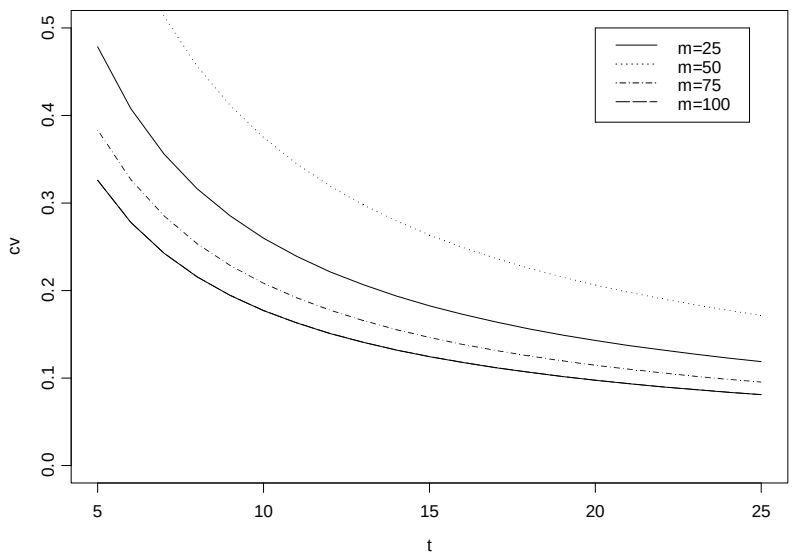

Figure 3: The cv of abundance estimates based on cumulative mark-recapture data, by year of capturing. Each year m whales in a population of $N = 100000$ are genetically marked after the catching season where $C = 600$ individuals are taken. Natural mortality is $M = 0.044$.

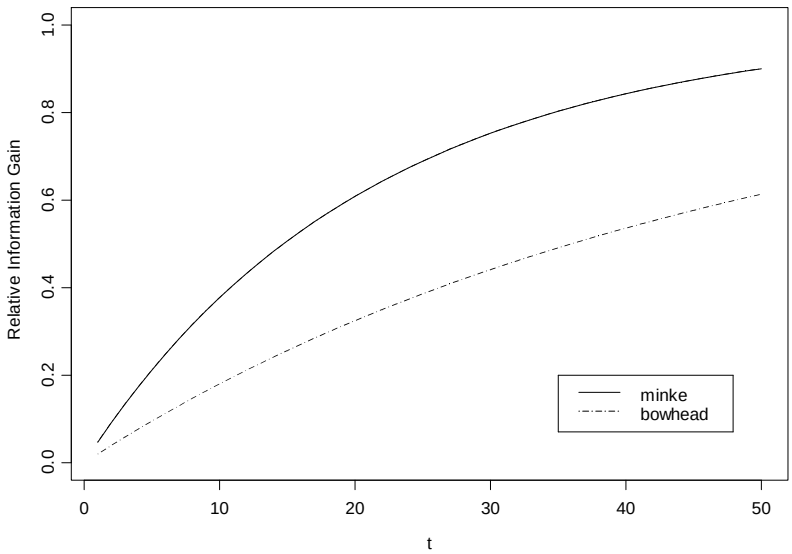

Figure 4: Information gain relative to maximum information gain in the abundance estimator based on a continued program of biopsy sampling and genotyping of harvested whales. For minke whales, $N = 100000$, $C = 600$, $M = 0.044$ and $m = 50$. For bowheads $N = 10000$, $C = 60$, $M = 0.017$ and $m = 10$.