

Technical Report (not peer reviewed)

Use of genetic data for abundance estimate purposes: a brief review of methods and case studies by the Institute of Cetacean Research

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ABSTRACT

Sighting surveys by the line transect method is the most used approach to estimate abundance in whales. Sighting surveys have some limitations associated with bad weather and sea conditions, and with the difficulty to cover all areas of distribution of the stocks. Given these limitations, alternative methods are being investigated for estimating the abundance of whales. This paper presents an overview of the current genetic methods for abundance estimation in whales. These methods are based on the mark-recapture (MR) approach and can be divided into two groups: i) those based on the history of individual identification (genotyping based on biopsy samples), and ii) those based on kinship information including paternity analysis and close-kin MR (based on biopsy samples and/or catches). This paper also presents information on case studies conducted by the Institute of Cetacean Research.

INTRODUCTION

Abundance estimation is one of the most important sources of information required for the conservation and management of whales. The analysis of sighting data collected by the line transect (LT) method (Buckland *et al.*, 2001) is the most common approach for estimating the abundance of whales. However, the use of this method has some limitations. For example, bad weather and sea conditions can prevent the surveys, while some areas are inaccessible to the surveys (e.g., polynyas in the Antarctic or territorial waters of other countries).

The mark-recapture (MR) method (Hammond, 1986; Pollock *et al.*, 1990) based on Discovery-type tags is another method used for abundance estimation. However, this method depends on whaling operations for the recovery of the tags, and this has been limited in recent years. MR methods can be used for individual whales identified by natural marks (photo-identification), however not all species have distinctive marks for individual identification, and the method would not be practical for abundant populations.

Given these limitations, alternative methods for abundance estimation of whales are being explored. In recent years, several methods for abundance estimation based on genetic individual identification and kinship inference have been reported. This paper presents an overview of those methods and outlines some case studies conduct-

ed by the Institute of Cetacean Research (ICR).

BASIC CONCEPT OF MARK-RECAPTURE

The MR method is widely used in ecology, particularly to estimate population size and some biological parameters such as survival rates. The MR method relies on sampling and re-sampling individual animals. A capture history simply describes whether or not an animal was captured in a series of sampling occasions during a period of data collection. It is usually represented by a series of 1 (captured) and 0 (not captured). The key idea of the MR method is to determine the ratio of marked individuals to unmarked individuals in the target population, i.e., estimate p (capture probability) from the proportion of marked animals that are recaptured. Figure 1 shows the situation of marks and mark-recaptures in two sampling occasions (two-sample estimator).

In Figure 1, M is the number of individuals marked in a population in the first year; c is the total number captured in the second year (with and without a mark); R is the number of captured in the second year that are marked (recaptured); and N is the size of the population at the time of marking and release.

The simplest MR method is the ‘Petersen method’ also known as ‘Lincoln method’ (Seber, 1982):

$$\frac{R}{c} = \frac{M}{N}.$$

The proportion of marked animals in the second time R/c is an estimate of the probability of capturing individual (\hat{p}), so that:

$$\hat{N} = \frac{M}{\hat{p}}.$$

Chapman's modification of Petersen's two-sample estimator (Chapman, 1951) is more appropriate in situations of small sample sizes, and is expressed as follows:

$$N = \frac{(M+1)(c+1)}{R+1} - 1.$$

Here,

M =number of individuals captured in the first year;

c =number of individuals captured in the second year;

R =number of individuals captured in both years.

Multiple sampling occasions

In the case of the two-sample estimator in Figure 1, the assumption of 'closed population' is adopted (births, immigration, emigration and death are not considered). For multiple sampling occasions involving a long period of time, the assumption of 'open population' is more appropriate, and immigration, emigration, birth and death should be considered (Figure 2).

In the case of multiple sampling occasions, the Jolly-Seber (JS) model (Jolly, 1965; Seber, 1965), an open population model, is the most appropriate. This model is very flexible and, in addition, can provide estimates of survival, recruitment and population growth rates.

There are a number of formulations based on the JS for estimating abundance and related parameters, such as the 'POPAN,' Link-Barker and Pradel recruitment, and the Burnham JS and Pradel- λ formulations. In particular, the POPAN formulation (Schwarz and Arnason, 1996) can provide abundance and net births by using the full likelihood approach. Net birth refers to all animals that enter after sampling occasion i and survive until sampling occasion $i+1$.

ABUNDANCE ESTIMATES BASED ON GENETIC DATA

The main advantages of using genetic tags for individual identification and abundance estimates based on MR are that: i) they are permanent and ii) they exist in all individuals. It is important that the genetic approach for individual identification and kinship inferences are reliable. The genetic basis for individual identification and kinship inferences is shown in Taguchi (this issue).

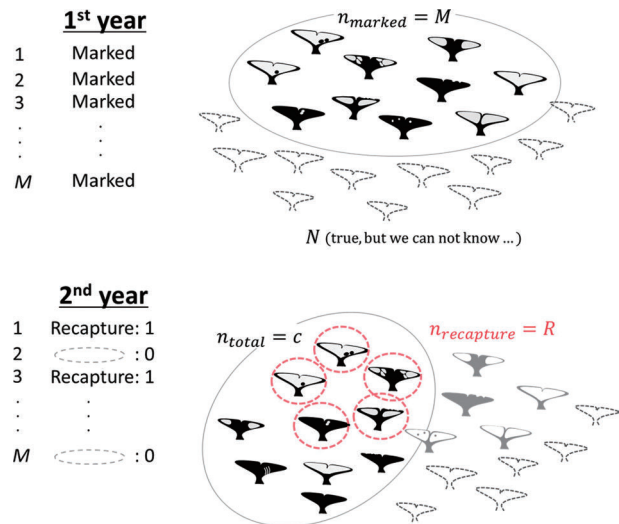


Figure 1. Diagram showing the basic idea of the MR method based on individual identification of humpback whales by photographic matching.

Methods based on the history of individual identification

The most common approach for genetic individual identification is based on biopsy sampling and genotyping, based on a number of nuclear marker loci. One of the most used markers is microsatellite DNA. If two biopsy samples, taken in different occasions/locations present the same genotype, then it is assumed that those biopsies were taken from the same individual (see Taguchi, this issue).

Some studies are presented here as examples of abundance estimates in whale populations based on biopsies, genetic individual identification and the MR methods. Palsbøll *et al.* (1997) conducted an analysis of six microsatellite loci for 3,060 skin samples collected from humpback whales throughout the North Atlantic. They detected 2,368 unique genotypes and, because the samples with identical genotypes were of the same sex, they considered that the 3,060 samples represented 2,368 individual whales. There was a total of 692 'recaptures.' The abundance and its confidence intervals (CI) were estimated based on the data collected in 1992 and 1993 and the two-sample estimators. The abundance was estimated at 4,894 (95% CI: 3,374–7,123) for males and 2,804 (95% CI: 1,776–4,463) for females.

Based on 354 biopsy samples collected from the New Zealand subantarctic southern right whales during the austral winter from 1995 to 1998, Carroll *et al.* (2011) were able to amplify 302 samples with 9–13 microsatellite loci. They identified 235 unique individuals during these four winter surveys. They estimated the superpopulation abundance using the POPAN JS model,

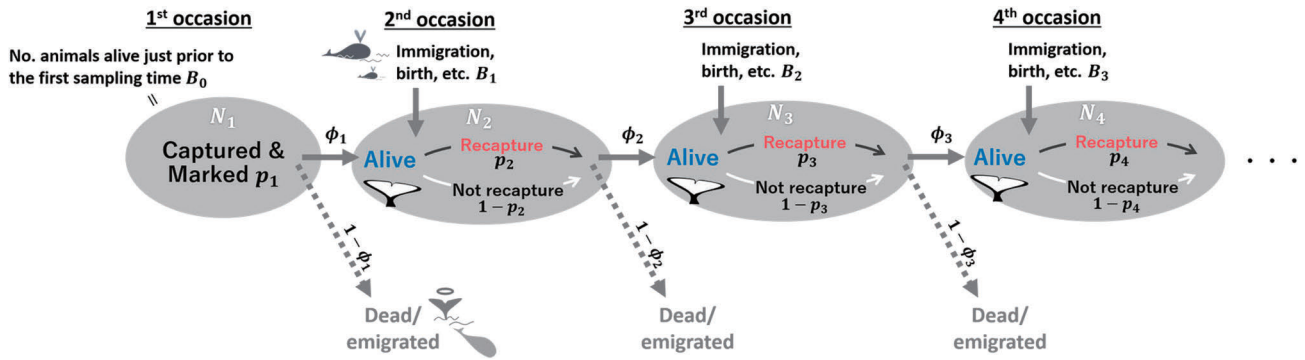


Figure 2. Diagram showing the situation of multiple sampling under the assumption of open population. A population changes in number and density due to births, deaths, immigration and emigration. Note that, ϕ_i represent the probability of (apparent) survival until the next sampling occasion; p_i is the probability of being captured and re-captured; B_i is the net number of new individuals joining the study area (modified from <http://www.phidot.org/software/mark/docs/book/pdf/chap12.pdf>).

which provided an estimate of 910 non-calf whales (95% CI: 641–1,354) in 1998.

Methods based on kinship information

An additional advantage of DNA tags is that they contain information about kinship among individuals. Hence, kinship relationship can be used for abundance estimates based on the classic MR using ‘recapture of self’ to ‘recapture of closely-related kin’. Several studies used DNA profiles to detect instances of paternity or other kinship relationships in whale populations (see Taguchi, this issue). For this approach, samples obtained from biopsy sampling as well as from catches can be used.

Paternity analysis

For the aim of paternity inference, Marshall *et al.* (1998) derived likelihood ratios with codominant markers taking account of typing error, and defined a statistic Δ for resolving paternity. The likelihood ratio can be written as:

$$L(H_1, H_2|D) = \frac{P(D|H_1)}{P(D|H_2)},$$

In this formulation, $P(D|H_i)$ is the probability of obtaining data D , i.e., genotypes of offspring, mother and potential father at a particular locus, under hypothesis H_i ($i=1, 2$). The hypothesis of H_1 is that the potential father is the true father, and this is tested against hypothesis H_2 wherein the potential father is an unrelated individual selected at random from the population.

Nielsen *et al.* (2001) presented a new method for paternity analysis in natural populations based on genotypic data that can take the sampling fraction of putative parents into account. They developed an approach for estimating parentage probabilities for paternity assignment, which is a Bayesian alternative to the method developed

by Marshall *et al.* (1998). They used the term ‘parentage probability’ to describe the posterior probability that a particular individual/putative father might be the actual father of a known offspring. They applied the method to genotypic data (six microsatellite DNA loci) collected from North Atlantic humpback whales.

The method of Nielsen *et al.* (2001) is briefly described here following the notations of the authors. They noted that the objective was to estimate the posterior probability that a particular individual might be the father of a known offspring. Let $I_j(i)$ indicate the event that the j th potential father is the father of the i th offspring. The i th maternal genotype is M_i , the associated genotype of the offspring is O_i , the genotype of j th potential father is F_j , and A is the matrix of allelic frequencies for all loci. If n of N males on the breeding ground were sampled, the posterior probability of paternity could be calculated as:

$$\Pr(I_j(i)|M_i, F, A, N) = \frac{\Pr(O_i|M_i, F_j)}{\sum_{j=1}^n \Pr(O_i|M_i, F_j) + (N-n)\Pr(O_i|M_i, A)}.$$

In this formulation $\Pr(O_i|M_i, F_j)$ is the shorthand notation for $\Pr(O_i|M_i, F_j, I_j(i))$. $\sum_{j=1}^n \Pr(O_i|M_i, F_j)$ refers to the sum of the probability that i th fetus has j th potential father as it’s father when i th maternal genotype and j th potential father are given. Assuming Mendelian segregation and independence among loci, the probability of an observed offspring genotype, given the maternal genotype and the genotype of a particular potential father $\Pr(O_i|M_i, F_j)$, could be calculated using standard methods (e.g., Thompson, 1975; 1976). Likewise, $\Pr(O_i|M_i, A)$ can be calculated assuming Hardy-Weinberg equilibrium and independence among loci (linkage equilibrium). $(N-n)\Pr(O_i|M_i, A)$ refers to the probability of the i th

fetus's genotype given the i th mother's genotype. In estimating the posterior probability that a potential father is the father of an offspring, assumptions need to be made regarding the prior probability of a potential father being the father. In the absence of other information, it is assumed that the prior probability that a particular male is the father is $1/N$, where N is the number of potentially breeding males in the breeding area (Nielsen *et al.*, 2001).

Here, assuming independence among offspring, the likelihood function for N can be calculated as:

$$L(N) \propto \prod_i \Pr(\mathbf{O}_i | \mathbf{M}_i, \mathbf{F}, \mathbf{A}, N) \\ = \prod_i \left(\frac{(N-n)}{N} \Pr(\mathbf{O}_i | \mathbf{M}_i, \mathbf{A}) + \frac{1}{N} \sum_{j=1}^n \Pr(\mathbf{O}_i | \mathbf{M}_i, \mathbf{F}_j) \right), \\ N \geq n.$$

The maximum-likelihood estimate of N and the confidence interval is provided, for example, using parametric bootstrapping. Note that the estimate based on this approach such as parent-offspring genotypes is an estimate of the current (i.e., at the time of sampling) male population size. To estimate the total abundance of the target population/species, additional information is required. For example, the proportions of males and females, and the sexual maturity of whales from the sample, under the assumption that the sample was representative of the true population.

Based on the method above, the maximum-likelihood estimate of N was 6,540 breeding male humpback whales (95% CI: 3,700–17,000) using parametric bootstrapping (Nielsen *et al.*, 2001).

CKMR method

CKMR is a recent extension of the ordinary MR methods used to estimate animal abundance and other population parameters. The CKMR approach was first described by Skaug (2001) working on microsatellite data (10 loci) of North Atlantic common minke whales. He derived an estimator for the total population size based on the number of parent-offspring pairs (POPs).

Subsequently Bravington *et al.* (2016a) extended the classic MR framework (Lincoln-Petersen type estimator mainly) by incorporating close-kin information. Whereas ordinary MR methods only consider the subsequent identification of the same animal as a recapture, CKMR expands this by also viewing the genetic identification of a relative (e.g., parent-offspring, full-sibling, half-sibling) as a recapture.

Below is the simplest version of the CKMR by Bravington *et al.* (2016a). This is a two-sample estimator for the

adult population size, which is the close-kin version of the Lincoln-Petersen population size estimator:

$$\widehat{N}_A = \frac{2n_j n_A}{H}. \quad (1)$$

Consider a sample of n_j juveniles and n_A adults from the same population. Each sampled juvenile can be considered a 'mark' of its two adult parents. The genotype of each of the n_j juvenile samples is compared to each of the n_A adult samples, to check if a 'mark' is recaptured. The probability that the adult happens to be one of the juvenile's two parents is $2/N_A$, where N_A is adult population size. The expected number of parent-offspring pairs across all $n_A \cdot n_j$ comparisons is then $2n_A n_j / N_A$. Equating this to the observed number of parent-offspring pairs gives the CKMR version of the Lincoln-Petersen estimator. Hence, if the entire set of $n_j \times n_A$ comparisons yields H which is the number of parent-offspring pairs, then adult abundance can be estimated as eq. (1).

In a more realistic setting, some types of kinship probabilities are likely to be present, and therefore, an explicit statistical MR model is required. That is, the prior probability that a pair is a POP is set by a population dynamics model, which accounts for pair-specific data, and which includes demographic parameters such as adult abundance, individual survival probability, age of maturity, per capita birth rate and probably age-specific fecundities.

For example, probability that individual i with covariates z_i (date of capture for example) is the mother of individual j with covariates z_j is represented as:

$$P(i \text{ is } j\text{'s mother} | z_i, z_j) \\ = E \left(\frac{i\text{'s reproductive output in } j\text{'s year of birth}}{\text{Total female reproductive output in } j\text{'s year of birth} | z_i, z_j} \right)$$

where $E()$ is the expected value and the absolute abundance (of females) now enters implicitly through the denominator.

Not only parent-offspring (PO) but also other kinship relationships such as half-sibling can be considered in the CKMR. A pairwise comparison between individuals i and j gives rise to a kinship category K_{ij} taking values from a discrete set $k = \{PO, HS, \dots\}$ (see also Taguchi (this issue)). These probabilities are the building blocks of the pseudo-likelihood shown below.

Demographic parameters can be estimated from the log-likelihood summed over all pairwise comparisons. The joint distribution of $\{K_{ij}; 1 \leq i < j \leq n\}$ is too complicated to permit the construction of a full likelihood. Instead, a pseudo-likelihood approach (Skaug, 2001; Bravington *et al.*, 2016a) which involves only the marginal probabili-

ties of the K_{ij} in eq. (2) was used.

$$l_P(\theta) = \sum_{1 \leq i < j \leq n} \log P(K_{ij} = k_{ij} | z_i, z_j; \theta). \quad (2)$$

Let ϑ denote the vector of all parameters that govern the basic quantities, for example, total population size (males and females): N , individual survival probability: φ , per capita average birth rate: β and capture probability at a given sampling occasion: p).

The CK greatly expands the scope of MR because a variety of samples can be used, including biopsy samples and samples from catches. However, age information is essential for precise CKMR estimates because it identifies the time of 'marking', which is the year the sampled animal was born.

Bravington *et al.* (2016b) used the approach above for the case of the southern bluefin tuna, using microsatellite data at 20–25 loci.

CASE STUDIES BY THE ICR

Based on the histories of individual identification

Pastene *et al.* (2018) examined a total of 157 biopsy samples of southern right whales collected by IDCR/SOWER and JARPA/JARPAII surveys in austral summer between 1987/88 to 2013/14 in the longitudinal sector between 80°E and 135°E (Figure 3). These southern right whales are associated with the South West Australia population.

Biopsy samples were examined with 14 microsatellite DNA loci. After removing four duplicates, the sample sizes for the individual identification became 153. Eight incidences of individual matching ('mark-recapture') were detected (four males and four females). Individual matching by multilocus genotypes was supported by mitochondrial DNA analyses (same haplotype), sex determination (same sex), and in two cases where pictures were available, by photo-identification. Estimate of abundance

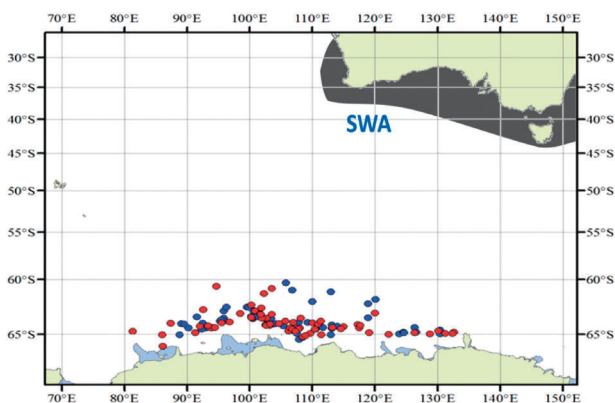


Figure 3. Geographical distribution of southern right whales in Area IV examined by Pastene *et al.* (2018). Red: females; Blue: males.

was based on the POPAN model implemented in RMark (Laake, 2013). This preliminary analysis considered the assumption of constant apparent survival, constant probability of capture and constant probability of entry through the years.

The results of the preliminary analyses showed similar annual abundance estimates to those obtained by sighting data in the same area and a similar period. For example, the estimate of abundance by the genetic 'mark-recapture' method was 1,619 (95% CI: 868–3,151) individuals for 2015/16, similar to the most recent (2007/08) sighting survey abundance estimate of 1,557 (95% CI: 871–2,783) individuals using the LT method in the same area.

Future analyses

The analysis conducted on southern right whales assumed constant apparent survival rate, constant capture probability, and constant probability of entry through the years. Some additional investigations are required to evaluate the effect of changing these assumptions on the abundance estimates. State-space models and hierarchical Bayesian approach have already been proposed as a convenient and flexible framework for specifying stochastic models for the dynamics of wild animal populations (Gimenez *et al.*, 2009; Kéry and Schaub, 2011; Hendrix *et al.*, 2012), and these models could be used for southern right whales in the future. Such models consider individual differences of the survival rate. Furthermore, the detection/capture probability, as a random effect can be evaluated by the state-space model.

Genetic databases for Antarctic blue and humpback whales are available at the ICR, and the abundance estimation approach for southern right whales can also be used for these other species.

One issue with mark-recapture analyses, regardless of which method of individual identification is used, is that the study area must provide adequate opportunities for 'capturing' all individuals within a population. However, this is hardly feasible because many populations are widely and unevenly distributed. Therefore, for obtaining more accurate abundance estimates, applying analytical techniques that take account of unsampled locations are also suggested for future analyses (e.g., Frasier *et al.*, 2020). Also, more information on the biological features of the species, such as migration and habitat use patterns, are required.

Paternity analyses

Kanda *et al.* (2014) conducted a study on paternity in

Antarctic minke whales based on samples collected by JARPA and JARPAII surveys. Specifically, genotypic data of a maximum of 12 microsatellite DNA loci were prepared from 137 fetuses collected from females captured during the 2003/04 JARPA survey, and their potential fathers were sought among 1,779 males collected from 2001/02 JARPA to 2010/11 JARPAII surveys.

One mother-fetus-father trio was detected using CERVUS (Marshall *et al.*, 1998), a computer program for assignment of parents to their offspring using genetic markers. This single match was used to tentatively estimate the mature male number in the Eastern Indian Ocean Stock (I stock) of Antarctic minke whales using the Petersen mark-recapture method modified by Chapman. Only mature males ($n=677$) (sexual maturity criteria of Kato, 1987) were used in the estimates.

The abundance estimate of the mature male component of the stock was 46,782 (CV=0.572) animals. Assuming the mature/immature ratio and the sex ratio were 1:1, respectively, the total stock size was estimated as 187,128 animals. This estimate was higher than the JARPA/JARPAII (51,474) and the IDCR (151,174) sighting surveys estimates in similar areas. Kanda *et al.* (2014) noted that their analysis estimated total stock size, while the JARPA/JARPAII and IDCR analyses estimated the number of individuals distributed in the research area based on sighting surveys, which would explain the differences.

Ohashi *et al.* (*in-press*) further examined the population size of mature males of Antarctic minke whales based on paternity analysis. Their analyses were based on biological and genetic (microsatellite DNA at 12 loci) data collected by JARPAII in the Indo-Pacific region of the Antarctic. A total of 2,126 Antarctic minke whales taken in the austral seasons 2006/07, 2008/09, 2009/10, 2010/11 and 2011/12 were used in the analyses. Two assumptions on stock structure were considered, a single stock in the research area and two stocks in the research area (the I stock and the Western South Pacific Stock (P stock)).

For abundance estimation, the approach of Nielsen *et al.* (2001) outlined above was used. For the hypothesis of a single stock, the abundance of mature males was estimated as 68,874 (90% CI: 42,625–122,779). Using the proportion of male and immature whales of 0.436 and 0.254, respectively, the estimate of total population was 211,600 (90% CI: 130,953–377,210). This estimate was lower than that from the IDCR/SOWER sighting surveys (413,202) and of the same order of JARPA/JARPAII estimates in Areas IV and V (263,711).

Future analyses

Ohashi *et al.* (*in-press*) reported that there are some technical issues in their analyses on Antarctic minke whales that should be improved in the future. Firstly, there is a need to optimize the use of the available genetic data and solve issues, for example, on genotyping errors and missing allele information for some loci. The second issue is related to the assumptions of the stock structure hypothesis. The current hypothesis on stock structure of Antarctic minke whales suggests a transition sector shared by the two stocks rather than a hard longitudinal boundary between them as assumed in the paternity analysis. This transition sector should be considered in future paternity analyses.

In addition, Ohashi *et al.* (*in-press*) noted that future analyses should consider not only the relationship between mother/fetus and father, but also some other kinship relationships (e.g., half-sibling) following the work of Bravington *et al.* (2016a) outlined above. Therefore, the next challenge for the ICR research on this topic is the application of the CKMR method for abundance estimation, which optimizes the use of the available genetic data.

Comparison of abundance between MR and LT methods

As noted by Kanda *et al.* (2014) and Pastene *et al.* (2018), estimates of abundance, using the ordinary MR approach based on genetic data, refer to the total population/stock size. The estimates based on sighting data under the LT approach, refer to the abundance of animals in a specific area and a specific period of a survey. Then, the difference in estimates will depend on the sighting survey coverage and on the movement of individuals into and out of the sighting survey area (Hammond, 2010).

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REFERENCES

- Bravington, M.V., Skaug, H.J. and Anderson, E.C. 2016a. Close-kin mark-recapture. *Stat. Sci.* 31: 259–274.
- Bravington, M.V., Grewe, P.M. and Davies, C.R. 2016b. Absolute abundance of southern bluefin tuna estimated by close-kin mark-recapture. *Nat. Commun.* 7: 1–8.
- Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L. and Thomas, L. 2001. *Introduction to Distance Sampling: Estimating Abundance of Biological Populations*. Oxford University Press, Oxford. 432 pp.
- Chapman, D.G. 1951. Some properties of the hypergeometric

- distribution with applications to zoological sample censuses. *University of California Publications in Statistics* 1: 131–160.
- Carroll, E.L., Patenaude, N.J., Childerhouse, S.J., Kraus, S.D., Fewster, R.M. and Baker, C.S. 2011. Abundance of the New Zealand subantarctic southern right whale population estimated from photo-identification and genotype mark-recapture. *Mar. Biol.* 158: 2565–2575.
- Frasier, T., Petersen, S., Postma, L., Johnson, L., Heide-Jørgensen, M.P. and Ferguson, S. 2020. Abundance estimation from genetic mark-recapture data when not all sites are sampled: An example with the bowhead whale. *Glob. Ecol. Conserv.* 22: e00903.
- Gimenez, O., Bonner, S.J., King, R., Parker, R.A., Brooks, S.P., Jamieson, L.E., Grosbois, V., Morgan, B.J.T. and Thomas, L. 2009. WinBUGS for population ecologists: Bayesian modeling using Markov Chain Monte Carlo methods. pp. 883–915. In: D.L. Thomson, E.G. Cooch and M.J. Conroy (eds.) *Modeling Demographic Processes in Marked Populations*. Environmental and ecological statistics 3. Springer, New York. 1132 pp.
- Hammond, P.S. 1986. Estimating the size of naturally marked whale populations using capture-recapture techniques. *Rep. Int. Whal. Commn* (special issue) 8: 252–282.
- Hammond, P.S. 2010. Estimating the abundance of marine mammals. pp. 42–67. In: I.L. Boyd, W.D. Bowen and S. Iverson (eds.) *Marine Mammal Ecology and Conservation: a handbook of techniques*. Oxford University Press, New York. 431 pp.
- Hendrix, A.N., Straley, J., Gabriele, C.M. and Gende, S.M. 2012. Bayesian estimation of humpback whale (*Megaptera novaeangliae*) population abundance and movement patterns in southeastern Alaska. *Can. J. Fish. Aquat. Sci.* 69: 1783–1797.
- Jolly, G.M. 1965. Explicit estimates from capture-recapture data with both death and immigration-stochastic model. *Biometrika* 52: 225–247.
- Kanda, N., Goto, M. and Pastene, L.A. 2014. Paternity analysis on Antarctic minke whales using JARPA and JARPAII samples. Paper SC/F14/J07 presented to the IWC SC JARPAII Review Workshop, February 2014 (unpublished). 4 pp. [Available from the IWC Secretariat].
- Kato, H. 1987. Density dependent changes in growth parameters of the southern minke whale. *Sci. Rep. Whales Res. Inst.* 38: 47–73.
- Kéry, M. and Schaub, M. 2011. *Bayesian Population Analysis Using WinBUGS: A Hierarchical Perspective*. Academic Press, Waltham, Massachusetts. 554 pp.
- Laake, J.L. 2013. RMark: An R Interface for analysis of capture-recapture data with MARK. AFSC Processed Rep. 2013-01, 25 p. Alaska Fish. Sci. Cent., NOAA, Natl. Mar. Fish. Serv., 7600 Sand Point Way NE, Seattle WA 98115.
- Marshall, T.C., Slate, J., Kruuk, L.E.B. and Pemberton, J.M. 1998. Statistical confidence for likelihood-based paternity inference in natural populations. *Mol. Ecol.* 7: 639–655.
- Nielsen, R., Mattila, D.K., Clapham, P.J. and Palsbøll, P.J. 2001. Statistical approaches to paternity analysis in natural populations and applications to the north Atlantic humpback whale. *Genetics* 157: 1673–1682.
- Ohashi, Y., Goto, M., Taguchi, M., Pastene, L.A. and Kitakado, T. Evaluation of a paternity method based on microsatellite DNA genotypes for estimating the abundance of Antarctic minke whales (*Balaenoptera bonaerensis*) in the Indo-Pacific region of the Antarctic. *Cetacean Population Studies (in press)*.
- Palsbøll, P.J., Allen, J., Bérubé, M., Clapham, P.J., Feddersen, T.P., Hammond, P.S., Hudson, R.R., Jørgensen, H., Katona, S., Larsen, A.H., Larsen, F., Lien, J., Mattila, D.K., Sigurjónsson, J., Sears, R., Smith, T., Sponer, R., Stevick, P. and Øien, N. 1997. Genetic tagging of humpback whales. *Nature* 388: 767–769.
- Pastene, L.A., Hakamada, T., Acuña, P., Taguchi, M., Goto, M., Matsuoka, K. and Nishiwaki, S. 2018. Site-fidelity and movement ranges of southern right whales in Antarctic Area IV inferred from genetic tagging. Paper SC/67B/SH/06 presented to the IWC Scientific Committee, May 2018 (unpublished). 10 pp. [Available from the IWC Secretariat].
- Pollock, K.H., Nichols, J.D., Brownie, C. and Hines, J.E. 1990. Statistical inference for capture-recapture experiments. *Wildl. Monogr.* 6: 288–295.
- Schwarz, C.J. and Arnason, A.N. 1996. A general methodology for the analysis of capture-recapture experiments in open populations. *Biometrics* 52: 860–873.
- Seber, G.A.F. 1965. A note on the multiple-recapture census. *Biometrika* 52: 249–259.
- Seber, G.A.F. 1982. *The estimation of animal abundance and related parameters. 2nd Edition*. Griffin, London. 654 pp.
- Skaug, H.J. 2001. Allele-sharing methods for estimation of population size. *Biometrics* 57: 750–756.
- Thompson, E.A. 1975. The estimation of pairwise relationships. *Ann. Hum. Genet.* 39: 173–188.
- Thompson, E.A. 1976. Inference of genealogical structure. *Soc. Sci. Inform.* 15: 477–526.