

# Genetic relatedness of North Atlantic fin whale

## *Balaenoptera physalus* in Icelandic waters

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### ABSTRACT

One of the main problems to the genetic structure of highly vagile pelagic species such as the cetacean lies in their almost continuous habitat, the lack of information on the location of their breeding ground and their potential connectivity. The North Atlantic fin whale (*Balaenoptera physalus*) is no exception as it undertakes long-distance annual migration between high-latitude summer feeding locations and low-latitude winter mating locations. Despite the numerous genetic studies performed to investigate stock structure, the uncertainties remaining concerning the mating location and route of migration render any conventional genetic investigations challenging. Alternative methods such as the used of microsatellite loci for relatedness approach can however, shed more light into their migration pattern and relationship between individuals from different feeding location. A common alternative statistic used for such approach is the LOD score (logarithm of odd scores), which is easily calculated from a pair of DNA-profiles. In the present paper, we present analysis based on a newly developed algorithm using LOD score and implemented on individual fin whales samples collected during the commercial catches in 2009 and 2010 in Icelandic waters. In total, 8 pairs of related individuals were found within the 34 959 pair comparisons (a total of 15 individuals), among which 3 were classified as parent-offspring, 3 as half-siblings, grandparent-grandchild or uncle/aunt-nephew/niece pairs, and two as half-siblings, uncle/aunt-niece/nephew pairs.

KEYWORDS: BALAENOPTERA PHYSALUS, ATLANTIC OCEAN, GENETICS, MIGRATION, ICELANDIC FEEDING GROUNDS, RELATEDNESS ANALYSIS.

## INTRODUCTION

In the last decades, several population genetic studies have been carried out on the North Atlantic fin whale stocks (Bérubé *et al.*, 1998; Daníelsdóttir *et al.*, 1992; Daníelsdóttir, 1994; Daníelsdóttir *et al.*, 2005, 2006; Palsbøll *et al.*, 2004; Pampoulie *et al.*, 2008), yet uncertainties remain on the genetic structure of this species. Early genetic studies and studies on morphological characters have revealed significant divergence among some fin whale stocks in the North Atlantic which are also supported by tagging experiments and other non-genetic evidence (Árnason and Jónsdóttir, 1988; Árnason *et al.*, 1992; Bérubé *et al.*, 1998; Daníelsdóttir *et al.*, 1991, 1992; Daníelsdóttir, 1994; Jover, 1987, 1991; Gunnlaugsson and Sigurjónsson, 1989; Sigurjónsson and Gunnlaugsson, 1985; Sigurjónsson *et al.*, 1991; Víkingsson and Gunnlaugsson, 2006). On the contrary, a genetic analyze using neutral markers failed to show any significant genetic structure at feeding grounds in the North Atlantic (Pampoulie *et al.*, 2008). Although the contrasting results of these studies can find their origin in the nature of the genetic markers used as well as in the history of the North Atlantic colonisation by the fin whale (Pampoulie *et al.*, 2008), genetic studies, have so far, failed to resolve stock discrimination issues in this species.

Most of the available data used for these genetic studies have been collected at feeding grounds which might be composed of a mixture of several distinct populations, and therefore indirect methods of gene flow, which were supposed to offer an alternative approach to assess gene flow among potential cetacean sub-populations, have proved unsuccessful. However, microsatellite loci can also be used to study individual relatedness within and among populations, which remains an alternative approach to investigate potential reproductive success differences among group of individual and/or migration patterns of individual North Atlantic fin whale (see Skaug and Øien, 2005). A common alternative statistic used for a given hypothesis about relatedness is the LOD score (logarithm of the odds score), which is easily calculated from a pair of DNA-profiles (Skaug *et al.*, 2010). In the present paper, we analysed 267 DNA-profiles at 15 microsatellite loci and look for relatedness among individual fin whales within Icelandic waters. Three kind of relationships were investigated, half-siblings, parent-offspring and first cousins.

## MATERIALS AND METHODS

All the genetic protocols used during this study were previously described in Pampoulie *et al.* (2012) and followed the IWC guidelines (see Tiedemann *et al.*, 2012. SC/64/SD4 for an update).

Relatedness analyses were performed using the genetic profiles ( $n = 267$ ) previously analyzed and originating from the commercial catches from 2009 and 2010 (Pampoulie *et al.*, 2012). In addition, 23 mothers carried a foetus and the foetus DNA profiles were therefore added to the original dataset presented. Because the LOD score method highly depends on matching of alleles, all individuals with missing alleles at certain loci were deleted from the dataset prior to the analyzes. A total of 25 individuals were removed from the analyzes, among which 1 foetus, 1 mother, and 22 other individuals.

All analyses and computations were done by using the program R (R Core Team, 2012), but script as well as algorithm are available upon request to the first author.

Detection of relatives was done by computing pairwise LOD scores for 265 individuals in the sample, for each relationships of interest, e.g. half-sibling, parent-offspring and first cousins. Let  $D_i$  and  $D_j$  be the DNA profiles of two individuals within our sample and consider the two mutually exclusive hypotheses  $H_0$ : *unrelated* and  $H_1$ : *relatedness of interest*. The LOD score is the logarithm of the ratio of the probabilities of the data under the two hypotheses (Balding, 2005). Under the assumption of Mendelian heritance rules the LOD score is defined by:

$$LOD = \log \left( \frac{P(D_i, D_j | \text{relatedness - of - interest})}{P(D_i, D_j | \text{unrelated})} \right)$$

$$= \log \left( \prod_{s=1}^{15} k_0 + k_1 \cdot \left( \frac{I(a_{i,s}^{(1)} = a_{j,s}^{(1)}) + I(a_{i,s}^{(1)} = a_{j,s}^{(2)})}{4 \cdot p(a_{i,s}^{(1)})} + \frac{I(a_{i,s}^{(2)} = a_{j,s}^{(1)}) + I(a_{i,s}^{(2)} = a_{j,s}^{(2)})}{4 \cdot p(a_{i,s}^{(2)})} \right) \right)$$

$(a_{i,s}^{(1)}, a_{i,s}^{(2)})$  denotes the genotype of individual  $i$  at locus  $s$ ,  $S$  is the number of independent markers and  $p(a_{i,s}^{(m)})$  is the population allele frequency for whatever type allele  $a_{i,s}^{(m)}$  is with  $m = 1, 2$  (Skaug *et al.*, 2010). The LOD

score for each relatedness of interest is attained by using the relevant coefficients,  $k_0$  and  $k_1$ . The relatedness coefficient  $k_j$  is defined as the probability of inheriting  $j$  alleles identical by descent given a certain relatedness (Balding, 2005).

**Table 1:** Relatedness coefficients

Relatedness of interest	$k_0$	$k_1$
Half-siblings*	0.5	0.5
Parent-offspring	0	1
First cousins	0.75	0.25

\*It is impossible to distinguish between half-siblings, a grandparent and a grandchild and an uncle/aunt-nephew/niece pair from genetic evidence alone (Weir, 2007).

According to Skaug *et al.* (2010), the LOD score for a specific relatedness will have optimal statistical power, among all possible tests, of rejecting the null hypothesis when individual  $i$  and  $j$  are indeed related in that certain way. For example the half-sibling LOD score of a pair of half-siblings will have greater statistical power than their parent-offspring LOD score.

Although a high LOD score indicates relatedness, it entails an issue of what should be considered to be high enough to reveal a significant relationship. That issue was accounted for by evaluating a single  $p$ -value with each LOD score with a Monte Carlo experiment built on a permutation method that Skaug *et al.* (2010) performed in the analysis of minke whale data. The high number of pairwise comparisons raised another statistical issue, the problem of multiple testing, e.g. significance of tests by chance due to the high rate of pairwise comparisons. This was addressed by a FDR procedure, e.g. the false discovery rate. The FDR procedure has been suggested to be more appropriate than the Bonferroni correction for example, as it takes the number of erroneous false discoveries of relatedness into account instead of only the question of whether any error was made (Benjamini and Hochberg, 1995).

The following procedure was applied to the fin whale data for each relatedness of interest:

- 1) The pairwise LOD score were computed using the formula mentioned above with the relevant relatedness coefficients.
- 2) The  $p$ -values for each LOD score were estimated via simulation. A total of 265 individuals were simulated by drawing allele types independently with replacement from a gene pool with the same allele frequencies as the original dataset, excluding the foetuses. Then, their pairwise LOD scores were computed. The  $p$ -values are computed by comparing the original LOD scores (real data) with the simulated ones (265 individuals simulated) but  $p_{i,j}$  can be described as the probability of attaining as extreme or more extreme LOD score than  $LOD_{i,j}$  just by chance.
- 3)  $p$ -values were adjusted for multiple testing by the FDR procedure. Benjamini's and Hochberg's (1995) FDR procedure is based on arranging the corresponding estimated  $p$ -values for each LOD score in increasing order  $p_{(1)} \leq p_{(2)} \leq \dots \leq p_{(n)}$ .  $q$  denotes the target false discovery rate,  $n$  is the number of pairwise comparisons and  $R$  is defined to be the largest value of  $r$  for which:

$$p_{(r)} \leq \frac{r}{n} \bullet q$$

Additional information such as age estimated from the ear plug and maturity assessed from the transition phase of the earplug were collected in order to estimate the kind of relationship observed.

## RESULTS AND DISCUSSION

In total, 8 pairs of related individuals were found within the 34 959 pairs comparisons (a total of 15 individuals as individual F10-020 was related to two individuals), when mother-foetus pairs were removed from the analyses (Table 2). The procedure was able to detect all mother-foetus pairs as a parent and an offspring at a false discovery rate at 0.05. Additional information from the analyses (detection level, tests performed) are available upon request to the first author of the paper.

**Table 2.** Results from all relatedness tests performed (half-sibling, parent-offspring, and first cousins coded as  $LOD_{h.sib}$ ,  $LOD_p$  and  $LOD_{cous}$  in the table) at  $q = 0.05$ .

Pairs	Related	$LOD_{h.sib}$	Parent-offspring	$LOD_p$	First cousins	$LOD_{cous}$
F10-020 and F10-026	Yes	5.07	Yes	7.40	Yes	3.28
F09-073 and F10-062	Yes	4.58	No	$-\infty$	Yes	3.00
F09-081 and F10-030	Yes	4.34	Yes	6.68	Yes	2.65
F09-047 and F10-079	Yes	3.70	No	$-\infty$	Yes	2.78
F10-020 and F09-040	Yes	3.70	No	$-\infty$	Yes	2.59
F10-089 and F10-140	Yes	3.64	Yes	5.47	No	2.28
F09-075 and F10-123	Yes	3.48	Yes	5.38	No	2.13
F09-91F and F10-100	Yes	3.42	Yes	5.43	No	2.00

Skaug *et al.* (2010) considered “half-sibling” search to be a reasonable choice for a first investigation of all type of close 1<sup>st</sup>- and 2<sup>nd</sup>- order relationships. That is in harmony with the result of this study as can be seen in Table 2. Biological information retrieved during the commercial catches such as age and estimation of maturity from the ear plug transition phase clarified the kind of relationships observed during the present study. Details on how this information could clarify the relatedness among individuals can be found below.

In order to come to a conclusion about a specific relatedness for each pair, the three different LOD scores have to be compared.  $LOD_{h.sib}$ ,  $LOD_p$  and  $LOD_{cous}$  compare the probability of the data under the hypothesis of a specific relatedness with the probability of the data under the null hypothesis of unrelatedness ( $H_0$ ). What is needed now is to compare the probability of the data under a specific relatedness with the probability of the data under another specific relatedness. That is done by simply subtracting one LOD score from the other since  $\log(a/b) = \log(a) - \log(b) = \log(a/c) - \log(b/c)$ . Results are then combined to available biological information.

#### **F10-020 and F10-026**

The fin whales F10-020, a 39.5 years old female that became mature when she was 10 years old, and F10-026, a 25 years old male, were concluded to be related from the  $LOD_{h.sib}$  at  $q = 0.05$ . They were also concluded as a mother and her son from  $LOD_p$  and as first cousins from  $LOD_{cous}$ . Since their age difference did not exclude that they could be a mother and son pair, the probability of the data under these specific relatedness hypotheses had to be compared. The LOD scores of F10-020 and F10-026 (see Table 2) imply that they were more likely to be a parent-offspring pair than half-siblings or first cousins.

#### **F09-073 and F10-062**

The individual whales F09-073, a 14.5 years old male, and F10-062, a 37.5 years old male with an estimated maturity age of 10.5 years, were concluded to be related from  $LOD_{h.sib}$ . They were also concluded as first cousins from  $LOD_{cous}$ . When the probabilities of the data under these specific relatedness hypotheses were compared then F09-073 and F10-062 seemed more likely to be half-siblings, a grandfather and his grandson or an uncle and his nephew than to be first cousins. Since their age difference was about 22 years (F10-062 was 36.5 years old in 2009), it was impossible to draw further conclusions about their relatedness.

#### **F09-081 and F10-030**

The individual whales F09-081, a 15 years old female, and F10-030, a 45 years old female with an estimated maturity age of 11 years, were to be concluded related from their  $LOD_{h.sib}$ . They were also concluded as a mother and a daughter from  $LOD_p$  and as first cousins from  $LOD_{cous}$ . Since their age difference did not exclude mother-daughter relations the probability of the data under these three specific relatedness hypotheses had to be compared. From Table 2 we can see that  $LOD_p > LOD_{h.sib} > LOD_{cous}$  so the conclusion was that F10-030 and F09-081 were likely to be a mother and her daughter.

#### **F09-047 and F10-079**

The individual whales F09-047, a 39 years old male with an estimated maturity age of 10 years, and F10-079, a 22 years old male, were concluded to be related from the  $LOD_{h.sib}$ . They were also concluded as first cousins from their  $LOD_{cous}$ . Comparison of those two LOD scores implies that F09-047 and F10-079 were more likely to

be half-brothers or a grandfather and his grandson or an uncle and his nephew than first cousins. Their age difference was 18 years (note that F10-079 was 21 years old in 2009) so no further conclusions could be drawn about their relatedness.

#### **F09-040 and F10-020**

The individual whales F09-040, a 20 years old female, and F10-020, a 39.5 years old female with an estimated maturity age of 10 years, were concluded to be related from the  $LOD_{h.sib}$ . They were also concluded as first cousins from their  $LOD_{cous}$ . Since their  $LOD_{cous}$  score was lower than their  $LOD_{h.sib}$  the conclusion was that F10-020 and F09-040 were more likely to be half-siblings or a grandmother and her granddaughter or an aunt and her niece than first cousins. Their estimated age difference was 18.5 years (F10-020 was 38.5 years old in 2009) so no further conclusions could be drawn about their relatedness.

#### **F10-089 and F10-140**

The individual whales F10-089, a 47 years old male with an estimated maturity age of 11 years, and F10-140, a 37.5 years old female, were concluded to be related from the  $LOD_{h.sib}$  and as a father and his daughter from their  $LOD_p$ . Here it becomes evident how important it was to take non genetic evidence into account. Comparison of their LOD scores indicates that these two whales were more likely to be a father and his daughter than half-siblings however the estimation of their age indicated that it was impossible since their age difference was less than 11 years. The conclusion is that F10-089 and F10-140 are either half-siblings or an uncle and his niece (or an aunt and her nephew) but grandfather and granddaughter relations can be ruled out because of the age difference.

#### **F09-075 and F10-123**

The individual whales F09-075, a 22 years old female with an estimated maturity age of 12 years, and F10-123, a 18.5 years old female, were concluded to be related from the  $LOD_{h.sib}$  and as a mother and her daughter from their  $LOD_p$ . Even though the genetic evidence implied that they were mother and a daughter, the conclusion was that F09-075 and F10-123 were either half-sisters or an aunt and her niece since their estimated age difference was only 4.5 years.

#### **F09-091F and F10-100**

The foetus F09-091F and F10-100, a 35.5 years old male with a maturity age of 11 years, were concluded to be related by the  $LOD_{h.sib}$  and as a parent and an offspring by their  $LOD_p$ . The genetic evidence suggested that F10-100 was more likely to be the father of F09-091F than a half-brother and the age of F10-100 did not exclude him from being the father of F09-091F. In this case, further auxiliary data was available, the DNA profile of the mother F09-091 which makes the computation of a paternity LOD score possible. The difference between a  $LOD_p$  and a paternity LOD score is that the latter one accounts for the mothers profile while the other one does not. Balding (2005) provides a good description of the computation of paternity likelihood ratios. The paternity LOD score for F10-100 and F09-91F is 8.17 while their parent-offspring LOD score was 5.43. By considering F10-100, F09-091 and F09-091F jointly as a parent-pair and their offspring, F10-100 can now be classified as the father of F09-091F with greater determination than when the genetic profiles of F10-100 and F09-091F were examined pairwise. The final conclusion was that F10-100 is the father of F09-091F as concluded by Pampoulie *et al.* (2012) when they searched for fathers of the foetuses in this same sample.

The final result of the analysis has been summarized in Table 3. The test procedure detected in all eight pairs of related individuals within the dataset of 34 959 pairs.

**Table 3.** Final investigation of relatedness among 8 pairs of individuals in Icelandic waters.

<b>Pairs</b>	<b>Conclusion</b>
F10-020 and F10-026	Mother and son
F09-073 and F10-062	Half-brothers / grandfather and grandson / uncle and nephew
F09-081 and F10-030	Mother and daughter
F09-047 and F10-079	Half-brothers / grandfather and grandson / uncle and nephew
F10-020 and F09-040	Half-sisters / grandmother and granddaughter / aunt and niece
F10-089 and F10-140	Half-siblings / uncle and niece / aunt and nephew
F09-075 and F10-123	Half-sisters / niece and aunt
F09-91F and F10-100	Father and offspring

To conclude, the test-procedure developed during this study seemed to be promising to investigate close-relationship among individuals captured within the same IWC “stocks” boundaries. By investigating relatedness in a three steps procedure (1-computation of LOD score, 2-simulation of  $p$ -values, 3-FDR procedure), we were able to find relationships among 15 individuals caught in 2009 and 2010 in Icelandic waters, exhibiting different types of relation, from grand parent to grand child, to parent and child. The results were promising and should be applied to large scale relatedness analyses and are now supported by estimation of  $p$ -values, a measure that until now was the drawback of such an approach.

## REFERENCES LIST

- Árnason, A., and Jónsdóttir, S., 1988. An electrophoretic study of cardiac esterases and proteins of fin whales (*Balaenoptera physalus*) from Icelandic and Spanish water, and sei whales caught off Iceland. Paper SC/39/Ba 6 presented to the IWC Scientific Committee, June 1988 (unpublished), 14pp.
- Árnason, A., Daniélsdóttir, A.K., Spilliaert, R., Sigurðsson, J.H., Jónsdóttir, S., Pálsdóttir, A., Duke, E.J., Joyce, P., Groves, V., and Trowsdale, J., 1992. A brief review of protein and DNA marker studies in relation to the stock identity of fin whales (*Balaenoptera physalus*) from Iceland and Spain. *Rep. Int. Whal. Commn* 42: 701-5.
- Balding, D.J., 2005. Weight-of-evidence for Forensic DNA Profiles. John Wiley & Sons Hoboken, NJ.
- Benjamini, Y., and Hochberg, Y., 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. *J. R. Statist. Soc. B* 57: 289-300.
- Bérubé, M., Aguilar, A., Dendanto, D., Larsen, F., Notarbartolo di Sciarra, G., Sears, R., Sigurjónsson, J., Urban-R., J., and Palsbøll, P.J., 1998. Population genetic structure of North Atlantic, Mediterranean Sea and Sea of Cortez fin whales, *Balaenoptera physalus* (Linnaeus 1758): analysis of mitochondrial and nuclear loci. *Mol. Ecol.* 7: 585-99.
- Daniélsdóttir, A.K., Duke, E.J., Joyce, P., and Árnason, A., 1991. Preliminary studies on the genetic variation at enzyme loci in fin whales (*Balaenoptera physalus*) and sei whales (*Balaenoptera borealis*) from the North Atlantic. *Rep. Int. Whal. Commn* (special issue 13): 115-24.
- Daniélsdóttir, A.K., Sigurjónsson, J., Mitchell, E., and Árnason, A., 1992. Report on a pilot study of genetic variation in skin samples of North Atlantic fin whales (*Balaenoptera physalus*). Paper SC/44/NAB16 presented to the IWC Scientific Committee, June 1992, 8pp.
- Daniélsdóttir, A.K., 1994. Genetic variation among different species and populations of baleen whales from the North Atlantic Ocean. Ph.D. Thesis, University College Dublin, Ireland. 308pp.
- Daniélsdóttir, A.K., Stefánsson, M.Ö., Thorgilsson, B., Jörundsdóttir, Th.D., Ragnarsdóttir, A., Árnason, A., Gunnlaugsson, Th., Víkingsson, G.A., Ólafsdóttir, D., Bérubé, M., Palsbøll, P.J., Øien, N., Witting, L., and Pampoulie, C., 2005. Genetic analysis of North Atlantic fin whales (*Balaenoptera physalus*): Is there more than one breeding unit at the feeding ground west off Iceland? Paper presented at the *International Whaling Commission (IWC) Scientific Meeting*, 30<sup>th</sup> May – 8<sup>th</sup> June 2005, Ulsan, Republic of Korea. IWC SC/57/PFI4, 12pp.
- Daniélsdóttir, A.K., Bérubé, M., Palsbøll, P.J., Stefánsson, M.Ö., Thorgilsson, B., Jörundsdóttir, Th.D., Ragnarsdóttir, A., Árnason, A., Gunnlaugsson, Th., Ólafsdóttir, D., Øien, N., Witting, L., Pampoulie, C., and Víkingsson, G.A., 2006. Genetic stock delineation of fin whales. Paper presented at the joint North Atlantic Marine Mammal Commission (NAMMCO) and International Whaling Commission (IWC) Scientific workshop on the catch history, stock structure and abundance of North Atlantic fin whales, 23<sup>rd</sup> March – 26<sup>th</sup> March 2006, Reykjavík, Iceland. SC/58/FW/3 – SC/M06/FW5. 25pp.
- Gunnlaugsson, Th., and Sigurjónsson, J., 1989. Analysis of the North-Atlantic fin whale marking data from 1979-1988 with special reference of Iceland. *Rep. Int. Whal. Commn* 39: 383-8.
- Jover, L., 1987. Biometrical discrimination between Icelandic and Spanish stocks of fin whales (*Balaenoptera physalus*). Paper SC/38/Ba3 presented to the IWC, 1989 (unpublished), 12pp.
- Jover, L., 1991. Reanalysis of morphometric differences between Icelandic and Spanish stocks of fin whales (*Balaenoptera physalus*). Paper SC/F91/F44 presented to the IWC Scientific Committee, February 1991 (unpublished), 9pp.
- Palsbøll, P.J., Bérubé, M., Aguilar, A., Notarbartolo-Di-Sciarra, G., and Rasmus, N., 2004. Discerning between recurrent gene flow and recent divergence under a finite-site mutation model applied to North Atlantic and Mediterranean Sea fin whale (*Balaenoptera physalus*) populations. *Evolution* 58: 670-5.
- Pampoulie, C., Daniélsdóttir, A.K., Bérubé, M., Palsboll, P.J., Árnason, A., Gunnlaugsson, Th., Ólafsdóttir, D., Øien, N., Witting, L., and Víkingsson, G.A., 2008. Lack of genetic divergence among samples of the North Atlantic fin whale collected at feeding grounds: congruence among microsatellite loci and mtDNA in the new Icelandic dataset. 17pp. SC/60/PFI11.
- Pampoulie, C., Ólafsdóttir, G., Hauksdóttir, S., Skírnisdóttir, S., Ólafsson, K., Magnúsdóttir, S., Chosson, V., Halldórsson, S.D., Ólafsdóttir, D., Gunnlaugsson, T., and Víkingsson, G.A., 2012. Mother-fetus pair analyzes in the Atlantic fin whale (*Balaenoptera physalus*): an insight into the migration pattern of the species? *J. Cetac. Res. Manage.* 12: 341-3.
- R Core Team, 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org/>.
- Sigurjónsson, J., Gunnlaugsson, Th., Ensor, P., Newcomer, M., and Víkingsson, G., 1991. North Atlantic Sightings Survey 1989 (NASS-89): Shipboard surveys in Icelandic and adjacent waters July-August 1989. *Rep. Int. Whal. Commn* 41: 559-72.
- Sigurjónsson, J., and Gunnlaugsson, Th., 1985. Further mark-recapture analysis of fin whales caught off Iceland with a note on stock identity and movements of the East-Greenland/Icelandic population. *Rep. Int. Whal. Commn* 5: 257-362.
- Skaug, H.J., and Øien, N., 2005. Genetic tagging of male North Atlantic minke whales through comparison of maternal and foetal DNA-profiles. *J. Cetac. Res. Manage.* 7: 113-17.
- Skaug, H.J., Bérubé, M., and Palsbøll, P.J., 2010. Detecting dyads of related individuals in large collections of DNA-profiles by controlling the false discovery rate. *Mol. Ecol. Res.* 10: 693-700.
- Tiedemann, R., Cipriano, F., Morin, P. A., Hoelzel, A. R., Palsbøll, P., Waples, R., Natoli, A., Bachmann, L., Postma, L., Double, M., Pampoulie, C., Skaug, H., Baker, C. S., and Jackson, J., 2012. Updated guidelines for DNA data quality control and error rate estimation, for genetic studies relevant to IWC management advice. (First presented at IWC-SC60; updated by RT, FC, PM, RW, and JJ April/May 2012), Paper SC/64/SD4 presented at the IWC, Panama City, Panama.
- Víkingsson, G.A., and Gunnlaugsson, Th., 2006. Stock structure of fin whales (*Balaenoptera physalus*) in the North Atlantic – Indications from non-genetic data. Paper presented at the joint North Atlantic Marine Mammal Commission (NAMMCO) and International Whaling Commission (IWC) Scientific workshop on the catch history, stock structure and abundance of North Atlantic fin whales, 23<sup>rd</sup> March – 26<sup>th</sup> March 2006, Reykjavík, Iceland. SC/58/FW/7 – SC/M06/FW7.
- Weir, B.S., 2007 Handbook of Statistical Genetics, volume 2, chapter Forensics, pages 1368-1390. Wile-Interscience, 3 edition.