Evaluating stock structure hypotheses using genetically determined close relatives: A simulation study on North Atlantic Fin whales

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Abstract

Certain facets of the population dynamics of a species are hard to quantify. In particular stock boundaries are often hard to estimate. This document discusses the application of a recent tagging method applicable when breeding populations overlap on feeding grounds and extends upon . The tagging is augmented with information on genetically determined close relatives. The proposed tagging method is studied using simulations. Statistics which can be used to compare these rivalling stock structure hypotheses, are introduced and contrasted. The simulation emulates competing stock structure hypotheses for North Atlantic–Fin whales (*Balaenoptera physalus*).

The results show that, in the case of North Atlantic–Fin whales, an acceptable level of discriminatory power is reached with 100 effective samples.

Introduction

When managing a marine resource a number of complicated processes interact. The management typically encompasses diverse economical and political objectives such as the maximization of the resources yield and maintaining employment security. Politics and economics aside a rational utilization of the marine resource is often desired, e.g. how much of the resource can be reliably harvested sustainably (Baldursson et al., 1996). For the exploitation of fish and marine mammals managers have, historically, focused typically on issues pertaining to stock assessment while important questions regarding stock structure and distribution remain unanswered.

Stocks have often been defined by management boundaries. These management boundaries set according to the distribution of the key species of commercial interest Halliday and Pinhorn (1990) potentially. This could lead to separate advice given to the same stock depending on the management area for obvious reasons. Therefore, when dealing with fish stocks, numerous methods have employed to test the accuracy of stock definition and borders. Tagging, both mark recapture (Rayner, 1940; Chenuil et al., 2000; Laurenson et al., 2005; Peakall et al., 2006; Hannesson et al., 2008) or satelite tracking (Mate et al., 2007; Víkingsson and Heide-Jörgensen, 2012; Horton et al., 2011; Matthews et al., 2011), is commonly used to identify individual and stock movement between (and within) areas. Mark–recapture experiments are however not always suited to track individual movements. For instance fish may not survive the marking, marks do not survive a moulting period (i.e. crablike animals) or larval straying between populations. There are also factor not directly connected to the biology of the species, for instance baleen whales where a moratorium has been in place since 1986 which has, for obvious reasons, made traditional mark–recapture analysis (almost) impossible. Satellite tracking methods have their own deficiencies. In Víkingsson and Heide-Jörgensen (2012) the longest tag duration for a minke whale was less than 4 months and therefore not suitable to monitor annual migration patterns.

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Even when tagging is possible it is not always sufficient to detect separate breeding populations. Breeding stocks can overlap on feeding grounds, as suggested by an analysis of otolith classification or genetic structure (Reynolds and Templin, 2004; Wennevik et al., 2008; Jónsdóttir et al., 2007). These results indicate that, if neglected, managing two (or more) separate breeding populations could have adverse effects, such as an overexploitation of one breeding population, without being detected by conventional assessment methods.Genetic differences have been used to determine separate breeding populations of marine mammals (Andersen et al., 1997; Bérubé et al., 2002; Parsons et al., 2006; Fontaine et al., 2007; Pampoulie et al., 2008). Despite considerable efforts through decades (Donovan, 1991), traditional population genetic studies have in many cases failed to give unequivocal answers to important questions concerning cetacean stock structure. A major obstacle for interpretations of these studies has been the fact that for most baleen whales the breeding grounds are unknown and sampling has thus been restricted to the summer feeding grounds. Furthermore, large baleen whales, such as the North Atlantic Fin whales, do not often exhibit sufficient genetic variability to detect separate breeding populations (Bérubé et al., 1998; Pampoulie et al., 2008). The possibility of two or more breeding populations can, however, not be ruled out as the hypothesized split occurred relatively recently and the stocks have not had time to detectably differentiate (Pampoulie et al., 2008).

In the absense of detectable genetic structures genetic tagging (as described by Palsbøll, 1999) or other genetic methods such as information on close relatives could be used to answer question related to stock structure (Skaug, 2001; Palsbøll et al., 2010; Nielsen et al., 2001), for instance the effect of larval drift between different breeding stocks Planes et al. (2009). A simulation experiment of its potential application in management of marine mammals can be found in Økland et al. (2010) where managment units are defined for geographically segregated stocks using genetically determined close relatives. The authors, however, note that their method would hardly be applicable to stocks that overlap on feeding grounds whilst separate on breeding grounds, as is common for baleen whales, due low discriminatory power.

Here a simulation study of a (genetic) mark–recapture experiment, that has been augmented using information on genetically determined close relatives, is described. The simulation is based on a marine mammal population, the North Atlantic Fin whales, where it is assumed that the animals migrate between feeding and breeding grounds where they overlap to some degree. The tagging experiment aims to answer important management questions regarding stock structure. Relevant stock structure hypothesis are introduced and constrasted using three test statistics. The resulting analysis provides a power analysis of the comparison of the competing hypotheses as function of sample size

Methods

The setting

The North Atlantic Fin whale is spread out accross the whole of the North Atlantic and in a recent TNASS survey (Pike et al., 2008) the total abundance in the Irminger sea was estimated to be around 25.000 (95% C.I. 18.186 – 30.214) animals in 2001. Commercial fin whale operations started in the late 19th century, however after, according catch series data, a collapse in fin whale abundance the Icelandic parliament issued a ban on all whaling activities in 1914. When whaling resumed in 1948 the fin whale stocks in Icelandic waters had made a significant recovery.Since 1986 a whaling moratorium has been in place. In 2009 the Icelandic government lifted the ban on commercial fin whaling and began issuing an annual quota of 150 fin whales.

Tagging studies in Icelandic on the North Atlantic Fin whales have suggested that fin whales exhibit some site fidelity between year. For management areas in and adjacent to the Irminger sea, that is East–Greenland (EG), West–Iceland (WI) and East–Iceland (EI), To two different stock structures hypotheses have been suggested that could explain the fin whale distribution. The first is a mixing hypothesis where it is assumed that the fin whales in the waters around Iceland and East–Greenland originate from three separate breeding stocks with no dispersion (no genetic

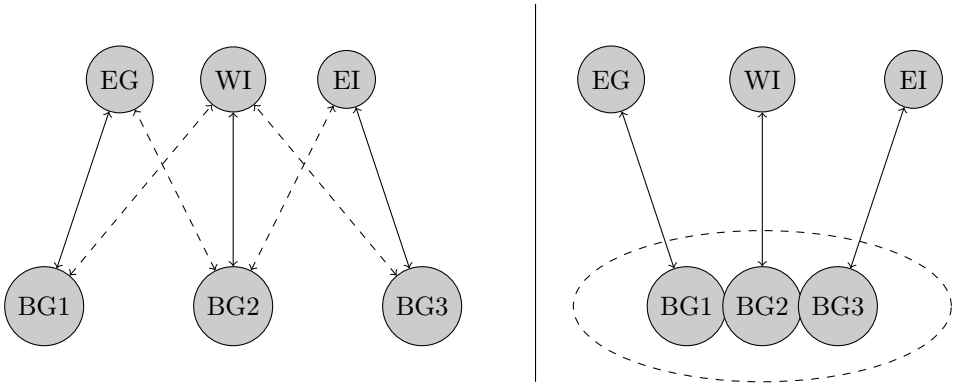

Figure 1: An overview of the competing stock structure hypotheses for the North Atlantic Fin whales in the Irminger sea. The figures illustrate three isolated breeding stocks with breeding grounds BG1, BG2 and BG3 that migrate to feeding grounds East of Greenland (EG), West (WI) and East of Iceland (EI). The figure on the left illustrates the mixing stock structure, where there is no gene sharing with some degree of overlap on the feeding grounds. The dashed line indicate movement from the breeding grounds to a feeding ground adjacent to the one which the majority of the substock population migrates to. The figure on the right shows the dispersion hypothesis, i.e. genetic sharing between the breeding stocks.

sharing) on the breeding grounds. It is assumed that the whales choose the next years feeding ground independently, i.e. with no memory, of where they were this year. The other hypothesis assumes that there is some degree of dispersion on the breeding grounds. Under this hypothesis whales choose their feeding ground based on last years feeding ground. An illustration contrasting the different feeding migrations patterns is shown in figure 1.

To compare the two stock structure hypotheses, dispersion and mixing hypothesis, a genetic tagging experiment (biopsy collection) in the East–Greenland subarea has been suggested. During which time, for a ten year period, a quota of 150 fin whales annually has been set in the West Iceland subarea. The tagging experiment is designed is order to reject the mixing hypothesis in favor of the dispersion hypothesis, if possible.

Simulation

The stock dynamics in this study were implemented in a computer program, `Rgadget` (Elvarsson et al., 2011), set up in such a way as to closely mimic the dynamics of the Baleen II model as described in Punt (1999). In the analysis which follows comparison will be made on the basis of two possible stock structures, mixing or dispersal type, as shown in figure 1. When mixing dynamics are assumed, separate breeding stocks overlap (to some fixed degree) on the feeding grounds, while dispersion denotes the permanent migration between breeding stocks.

The general dynamics of the population is (as in Punt, 1999) governed by the following. The stock size is determined by the following equations:

$$\begin{aligned}
N_{gj,t+1,0} &= \frac{b_{j,t+1}}{2} \\
N_{gj,t+1,a} &= e^{-M} \sum_{j \neq j'} \Big[(1 - D_{jj'})(N_{gjt,a-1} - C_{gjt,a-1}) + D_{j',j}(N_{gj't,a-1} - C_{gj't,a-1}) \Big] \\
N_{gj,t+1,x} &= e^{-M} \sum_{j \neq j'} \Big[(1 - D_{jj'})(N_{gjt,x-1} - C_{gjt,x-1} + N_{gjtx} - C_{gjtx}) + \\
&\qquad D_{j'j}(N_{gj't,x-1} - C_{gj't,x-1} + N_{gj't,x} - C_{gj'tx}) \Big]
\end{aligned} \tag{1}$$

where N_{gjta} is the number of animals of gender g, age $a < x$, $x = 25^+$ is the maximum age and stock j at the start of year t. C_{gjta} is the catch in numbers, b_{jt} the number of calves, $M = 0.08$ the natural mortality and $D_{jj'}$ is the stock dispersions from stock j to j'. Furthermore it is assumed that the stock are at their equilibrium density.

The stock distribution on feeding grounds is defined by a so called mixing matrix $\mathfrak{V} = V_{jk}$ where V_{jk} denotes the proportion of stock j that migrates to area k annually. Under the mixing hypothesis it is assumed that the central sub–stocks, even though separate on the breeding grounds, overlap on the feeding grounds. The feeding grounds have been split up into three distinct subareas. The subareas represent the main feeding ground for each of the central stocks. While 90% of the stocks individuals migrate to their own feeding ground, regardless of where they were last year, 5% migrate to each of the areas adjacent to their native feeding ground. The dispersion hypothesis assumes that individuals stray between sub–stocks while the sub–stocks migrate to a fixed area. In general the stock overlap (mixing) is according to:

$$\mathfrak{V} = \left(\begin{array}{c|ccc} & \mathbf{C1} & \mathbf{C2} & \mathbf{C3} \\ \hline \mathbf{EG} & 1-\alpha & \alpha & 0 \\ \mathbf{WI} & \alpha & 1-2\alpha & \alpha \\ \mathbf{EI} & 0 & \alpha & 1-\alpha \end{array} \right) \tag{2}$$

where the columns represent the breeding stocks (C1, C2, C3) and the rows feeding areas (EG, WI, EI). Under the mixing hypothesis $\alpha = 0.05$ while under the dispersion $\alpha = 0$. Under the dispersion $\alpha = 0.05$ while the annual straying between three sub–stocks is set according the following schema:

C1←C2	**C2→C3**	**C1↔C3**
0.05	0.3	0

with straying from **C1** and **C3** to **C2** defined to maintain equilibrium on feeding grounds.
where straying the reverse direction is then defined and estimated in order to to maintain equilibrium in the stocks sizes.

The recruitment to the stock is determined by the number of mature females in the stock population.

$$b_{jt} = B_j N_{fjt} \left[1 + A_j \left(1 - \left(\frac{N_{fjt}}{K_{fj}} \right)^{z_j} \right) \right] \tag{3}$$

where B_j is the average number of births per mature female and year in stock j, A_j and z_j are the resilience and compensation parameters, $N_{fjt} = \sum_{a=a_m}^{x} N_{fjta}$ is the number of mature females in stock j, $a_m = 6$ the age of first parturition and K_{fj} is the number of mature females in the pristine population. Values for the recruitment parameters are chosen such that the MSYR is 0.01 and is obtained at $0.72K_j$, where K_j the carrying capacity of stock j.

Commercial catches from the stocks are calculated in the usual manner:

$$\begin{aligned} C_{gjta} &= \sum_k F_{gkt} V_{jkt} S_{ga} N_{gjta} \\ F_{gtk} &= \frac{C_{gkt}}{\sum_{j'} V_{j'kt} \sum_{a'} S_{ga'} N_{gj'ta'}} \end{aligned} \tag{4}$$

where F_{gkt} is the harvest rate, S_{ga} is the gender specific selectivity formulated as Punt (1999):

$$S_{ga} = \frac{1}{1 + e^{-(a - a_{g50})/\delta_g}} \tag{5}$$

and V_{jkt} is the proportion of stock j in area k at year t. The values of the gender specific selection parameters are:

Selection:	Male	Female
δ_f	0.57	1
a_{50}	3.6	4.5

Tagging can, as noted above, be used to estimate stock migrations. Although here it is assumed that all tagging is made using data collected using genetic material such as skin samples it can fit well in with conventional mark–recapture analysis (Palsbøll, 1999) .The dynamics of the tagged sub–population in the simulations is the same as for the untagged population. For the sake of simplicity only a single tagging experiment, conducted in a single area, is considered in this analysis. The initial ($t = 0$) number of tagged animals is distributed for each stock j and each age a according to the equation:

$$\mathfrak{T}_{gj0a} = \frac{N_{gj0a} * \phi_0}{\sum_{gja} N_{gj0a}}, \tag{6}$$

where ϕ_0 is the total number of tagged animals. The expected number of animals recaptured is a function of the dynamics applied to the population, both tagged and untagged. The recaptures, $\hat{U}_t$, were considered to be distributed according to

$$\prod_t \frac{\Gamma(U_t + \hat{U}_t)}{\Gamma(\hat{U}_t + 1)\Gamma(U_t)} \left(\frac{\lambda}{1+\lambda}\right)^{U_t} \left(\frac{1}{1+\lambda}\right)^{\hat{U}_t}, \tag{7}$$

i.e. a negative binomial distribution with a dispersion[1] parameter U_t defined to be the predicted number of animals recaptured by commercial whaling fleets and $\lambda = 2$ controls the detection probability. Using a negative binomial distribution for the tag-recaptures, instead of a more commonly used poisson model, intended to allow for greater variation.

Comparing hypotheses

In the setting described above two different stock structure hypotheses are to be contrasted. To compare these stock structure hypotheses three potential methods of comparison are studied here.

- Time–trend analysis using regression.
- Total number of recaptured animals by area.
- Number of recaptured animals by area in relation to number of intra–related individuals within the catch.

To compare the two hypotheses using direct (genetic) tagging a negative binomial regression model for a time trend in the dispersion parameter can be fitted. The resulting model can be compared, using a likelihood ratio test, with a model with no time trend. The the rejection interval was set such that the type I error, i.e. the rejection probability when mixing is the true stock structure, was either 5% or 10%.

In genetic tagging augmented with information regarding genetically determined close relatives, such as described in Skaug (2001), a skin sample from a single whale can, in the case of NA–fin whales, effectively tag 2.5 – 3.5 other whales, as shown in Gunnlaugsson (2011 (submitted)). Using information on close relatives time trends in occurrance at feeding grounds are harder to detect. Intuitively this can be explained by noting that with a dispersing stock relatives are already present at both feeding grounds at the time of tagging. The total number of caught aninmals that are related to tagged individuals, i.e.

$$T_k = \sum_t \sum_{j \in \mathfrak{J}} T_{jkt} \tag{8}$$

where T_{jkt} is the number of animals related to the tagged animals from stock j, caught in area k at time t and $\mathfrak{J}$ denotes the set of breeding stocks. T_k should, given a similar degree of dispersion and mixing, be somewhat higher for dispersing stocks than mixing due to a similar argument as before.

[1] Not to be confused with stock dispersion

Untagged whales caught are also a source of information regarding the stock structure. The unobservable magnitude of genetic relatedness detected between all whales caught of stock j, denoted R_k, in area k is expected to be:

$$R_{jk} = \frac{c_{jk}(c_{jk}-1)}{2n_j} \tag{9}$$

where c_{jk} is number of animals caught in area k from stock j and where it is assumed one genetic relation can be detected per individual within a stock j of total size of n_j. Note that R_{jk} tends be smaller as n_j grows larger and the total number of relations detected $\left(\sum_j R_{jk}\right)$ becomes smaller with fixed abundance as the number of breeding stock decreases.

Using the information on related individuals one can augment equation 8 by calculating the following ratio for each area:

$$\rho_k = \frac{\sum_t \sum_{j\in\Im} T_{jkt}}{\sum_{j\in\Im} R_{jk}} \tag{10}$$

The above quantity should become larger for dispersing stocks as there is genetic interchange, even if the total number of effectively tagged individuals is similar.

For each of to the stock structure hypothesis the number of simulated datasets per hypothesis was 1000 for each number of tags. The number of tags in this experiment varied between 100 to 1500. The tag–recaptures were simulated using equation 7. The stock proportions within the catch (c_j from equation 9) were simulated using a multinomial distribution parametrised by the expected value of number of individuals caught from each stock. The distribution of the three test statistics was analysed and for the Null hypothesis, which is in this case the mixing hypothesis, the rejection interval was chosen in such a way that it would have a rejection probability of 0.05. Using simulated data based on the alternative hypothesis, which is the dispersion hypothesis, the power of the test was calculated as a function of the number of tags.

Results

The discriminatory performance of the various statistics discussed above are shown in figures 2, 3 and 4. Trend analysis using a negative binomial regression model, which assumes direct tagging of individuals, appears to have substantial problems with detecting the difference between the two hypotheses at these low numbers of tagged whales and mixing. Figure 2 shows that even with 400 direct tags the power to differentiate between the two is relatively low. In fact, in table 1 it can be seen that in order to get a power of 80% with a chance of Type I error of 5% a little over a thousand direct tags are needed. If, however, the requirement on type I error is loosened to 10% the the required number of tags to get a power of 80% is 700.

The other two metrics, the total number of recaptured animals (direct or related to tagged animals) as described by equation 8 and the ratio ρ of that to relatives in the catches (equation 10), show greater discriminatory power. The number of recaptured animals has the ability to distinguish between the mixing and dispersion hypotheses with close to 200 effective tags ($\tilde{1}00$ biopsy samples) with a power of > 80, as illustrated in table 2.

The ρ ratio adds information on the relatives in the catches. Figure 4 shows the discriminatory power to be fairly good, even with as few as 100 samples. According to the results in table 3 the power is well in excess of 80%.

Discussion

The analysis presented here illustrates a potential use of genetically determined close relatives when determining management units for large baleen whales. It adds to an already described methodology illustrated in Økland et al. (2010) by allowing for stock overlap in the feeding grounds.

When studying the NA–fin whale the methods described here compare favorably to conventional mark–recapture methods simply through the increase in effective number of samples. Genetically closely related individuals (matched pairs) may have split and dispersed over a longer period than the time lapse between the collection of the samples. This was not modeled here but would give additional strength.

Two sources of potential biases need to be mentioned regarding this study. Firstly it is assumed that the simulated whale populations are at their carrying capacity. This assumption is made merely out of convenience, as the whale populations are considered to be close to it, and should not influence the results dramatically. The simulated time period is relatively short compared to the lifespan of the whales, who enter the harvest at the average age of around 4 years and the production of the stock is rather low. The second source of bias is the fact that the stock abundances are assumed to be known that could, when included into the simulation study, decrease the power of the tests.

The level of the stock overlap, i.e. mixing rate, influences the results. At these really low levels the test statistics described in equations 8 and 10 perform considerably better than a regression model with a time trend. However it is expected that as the mixing rate increases the power of the time trend analysis would stay fixed while at the same time the power of the other two statistics would decrease. The effect on management in this particular case would however be reduced as the qouta assigned in the area West of Iceland would increase under the mixing hypothesis (IWC, 2012).

With close kin relationships such as utilized here one needs to take considerable care when deciding what level of close relation are included. On one hand it is a question of feasibility as the number of alleles needed for accurate detection of increases substantially as the order of relation increases. On the other hand it depends on the stock structure hypotheses under scrutiny. In this case it is expected, as noted earlier, that in the case of the North Atlantic fin whale the effective number of tags lies between 2.5 and 3.5 per skin sample which could increase the power of the tests by a similar factor. However if one were to study hypotheses such as male mediated DNA one would need to focus on mother offspring pairs.

References

L.W. Andersen, L.E. Holm, H.R. Siegismund, B. Clausen, C.C. Kinze, and V. Loeschcke. A combined dna-microsatellite and isozyme analysis of the population structure of the harbour porpoise in danish waters and west greenland. *Heredity*, 78(3):270–276, 1997.

Fridrik M. Baldursson, Ásgeir Daníelsson, and Gunnar Stefánsson. On the rational utilization of the icelandic cod stock. *ICES Journal of Marine Science: Journal du Conseil*, 53(4):643–658, 1996. doi: 10.1006/jmsc.1996.0085. URL `http://icesjms.oxfordjournals.org/content/53/4/643.abstract`.

M. Bérubé, A. Aguilar, D. Dendanto, F. Larsen, G. Notarbartolo di Sciara, R. Sears, J. Sigurjónsson, J. URBAN-R, and PJ Palsbøll. Population genetic structure of north atlantic, mediterranean sea and sea of cortez fin whales, balaenoptera physalus (linnaeus 1758): analysis of mitochondrial and nuclear loci. *Molecular Ecology*, 7(5):585–599, 1998.

M. Bérubé, J. Urbán, A.E. Dizon, R.L. Brownell, and P.J. Palsbøll. Genetic identification of a small and highly isolated population of fin whales (balaenoptera physalus) in the sea of cortez, mexico. *Conservation Genetics*, 3(2):183–190, 2002.

A. Chenuil, L. Crespin, L. Pouyaud, and B. Patrick. Movements of adult fish in a hybrid zone revealed by microsatellite genetic analysis and capture-recapture data. *Freshwater Biology*, 43 (1):121–131, 2000.

GP Donovan. A review of iwc stock boundaries. *Rept. Int. Whal. Commn., Special*, 13:39–68, 1991.

Bjarki Þór Elvarsson, Ásta Jenný Sigurðardóttir, Elínborg Ingunn Ólafasdóttir, Lorna Taylor, and Gunnar Stefánsson. Rgadget: A marine multispecies simulator. Unpublished manuscript, 2011.

M.C. Fontaine, S.J.E. Baird, S. Piry, N. Ray, K.A. Tolley, S. Duke, A. Birkun, M. Ferreira, T. Jauniaux, Á. Llavona, et al. Rise of oceanographic barriers in continuous populations of a cetacean: the genetic structure of harbour porpoises in old world waters. *BMC biology*, 5(1):30, 2007.

Th. Gunnlaugsson. Relatedness between samples quantifed and an optimal criterion for match detection approximated. *J.Cetacean Res. Manage.*, 11 (Suppl. 2)(587-627), 2011 (submitted).

RG Halliday and AT Pinhorn. *The delimitation of fishing areas in the northwest Atlantic*. Northwest Atlantic Fisheries Organization, 1990.

S. Hannesson, A. Jakobsdottir, J. Begley, L. Taylor, and G. Stefansson. On the use of tagging data in statistical multispecies multi-area models of marine populations. *ICES Journal of Marine Science*, 65(9):1762, 2008.

T.W. Horton, R.N. Holdaway, A.N. Zerbini, N. Hauser, C. Garrigue, A. Andriolo, and P.J. Clapham. Straight as an arrow: humpback whales swim constant course tracks during long-distance migration. *Biology letters*, 7(5):674–679, 2011.

IWC. Report of the sub–committee on the revised management procedure (rmp). *Journal of Cetacean Research and Management*, 13:88–95, 2012.

I.G. Jónsdóttir, G. Marteinsdottir, and S.E. Campana. Contribution of different spawning components to the mixed stock fishery for cod in icelandic waters. *ICES Journal of Marine Science: Journal du Conseil*, 64(9):1749–1759, 2007.

CH Laurenson, A. Johnson, and IG Priede. Movements and growth of monkfish *Lophius piscatorius* tagged at the shetland islands, northeastern atlantic. *Fisheries Research*, 71(2):185–195, 2005.

B. Mate, R. Mesecar, and B. Lagerquist. The evolution of satellite-monitored radio tags for large whales: One laboratory's experience. *Deep Sea Research Part II: Topical Studies in Oceanography*, 54(3):224–247, 2007.

C.J.D. Matthews, S.P. Luque, S.D. Petersen, R.D. Andrews, and S.H. Ferguson. Satellite tracking of a killer whale (orcinus orca) in the eastern canadian arctic documents ice avoidance and rapid, long-distance movement into the north atlantic. *Polar biology*, 34(7):1091–1096, 2011.

R. Nielsen, D.K. Mattila, P.J. Clapham, and P.J. Palsbøll. Statistical approaches to paternity analysis in natural populations and applications to the north atlantic humpback whale. *Genetics*, 157(4):1673–1682, 2001.

J.M. Økland, Ø.A. Haaland, and H.J. Skaug. A method for defining management units based on genetically determined close relatives. *ICES Journal of Marine Science: Journal du Conseil*, 67 (3):551–558, 2010.

Per. Palsbøll, M. Zachariah Peery, and M. Berube. Detecting populations in the âĂŸambiguousâĂŹ zone: kinship-based estimation of population structure at low genetic divergence. *Molecular Ecology Resources*, 10(5):797–805, 2010.

Per J. Palsbøll. Genetic tagging: contemporary molecular ecology. *Biological Journal of the Linnean Society*, 68(1-2):3–22, 1999.

C. Pampoulie, A. Danielsdottir, M. Berube, PJ Palsbøll, A. Arnarson, T. Gunnlaugsson, D. Olafsdottir, N. Øien, L. Witting, and GA Vikingsson. 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. *IWC SC/60/PFI11*, 2008.

K.M. Parsons, J.W. Durban, D.E. Claridge, D.L. Herzing, K.C. Balcomb, and L.R. Noble. Population genetic structure of coastal bottlenose dolphins (tursiops truncatus) in the northern bahamas. *Marine Mammal Science*, 22(2):276–298, 2006.

R. Peakall, D. Ebert, R. Cunningham, and D. Lindenmayer. Mark–recapture by genetic tagging reveals restricted movements by bush rats (rattus fuscipes) in a fragmented landscape. *Journal of Zoology*, 268(2):207–216, 2006.

Daniel G Pike, Thorvaldur Gunnlaugsson, Gísli A Víkingsson, and Bjarni Mikkelsen. Estimates of the abundance of fin whales (balaenoptera physalus) from the t-nass icelandic and faroese ship surveys conducted in 2007. *IWC SC/60/PFI13-revised*, 2008.

S. Planes, G.P. Jones, and S.R. Thorrold. Larval dispersal connects fish populations in a network of marine protected areas. *Proceedings of the National Academy of Sciences*, 106(14):5693–5697, 2009.

A.E. Punt. A full description of the standard baleen ii model and some variants thereof. *J. Cetacean Res. Manage*, 1:267–276, 1999.

G.W. Rayner. *Whale marking: progress and results to December 1939*. University Press, 1940.

J.H. Reynolds and W.D. Templin. Detecting specific populations in mixtures. *Environmental biology of fishes*, 69(1):233–243, 2004.

Hans J. Skaug. Allele-sharing methods for estimation of population size. *Biometrics*, 57(3):750–756, 2001.

Gísli Víkingsson and Mads Peter Heide-Jörgensen. Movement of minke whales, tracked by satellite in icelandic waters 2001-2010. Unpublished manuscript, 2012.

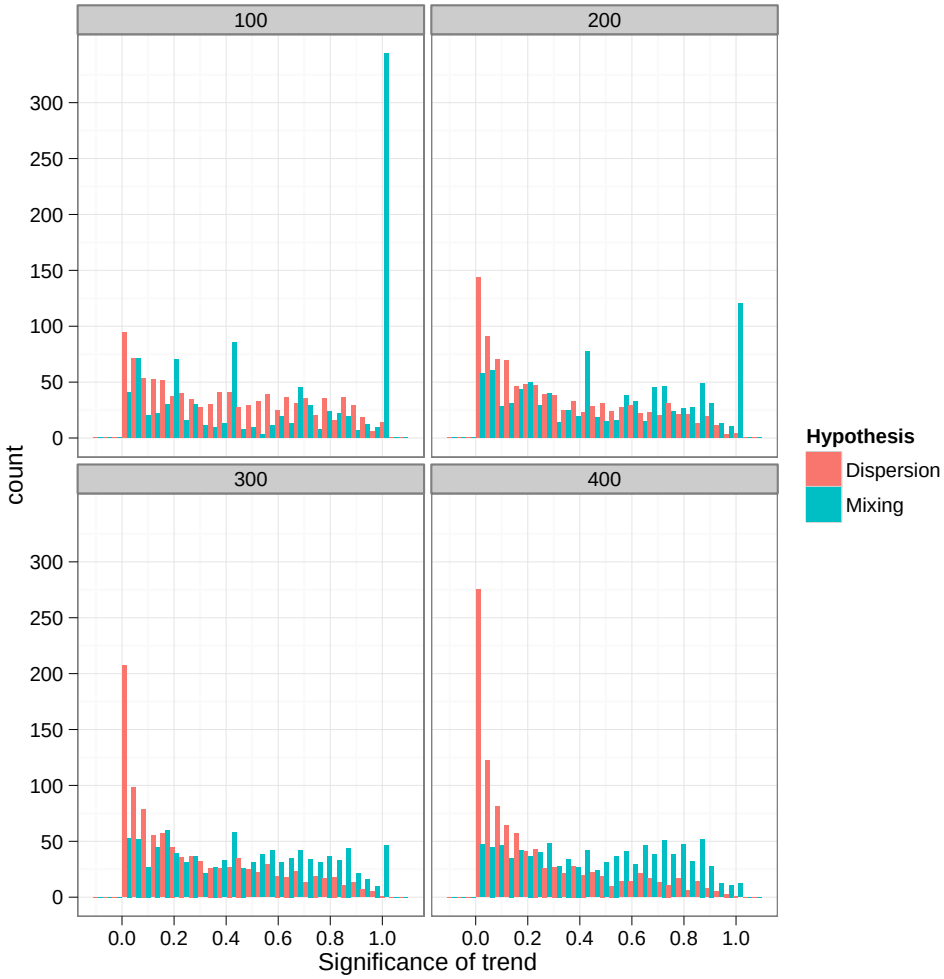

Figure 2: Histogram of the p-value for the test of significance of a time trend in a negative binomial regression model under the two competing hypothesis. The figure is faceted by the number of tags released in the EG sub–area.

V. Wennevik, K.E. Jørstad, G. Dahle, and S.E. Fevolden. Mixed stock analysis and the power of different classes of molecular markers in discriminating coastal and oceanic atlantic cod (gadus morhua l.) on the lofoten spawning grounds, northern norway. *Challenges to Marine Ecosystems*, pages 7–25, 2008.

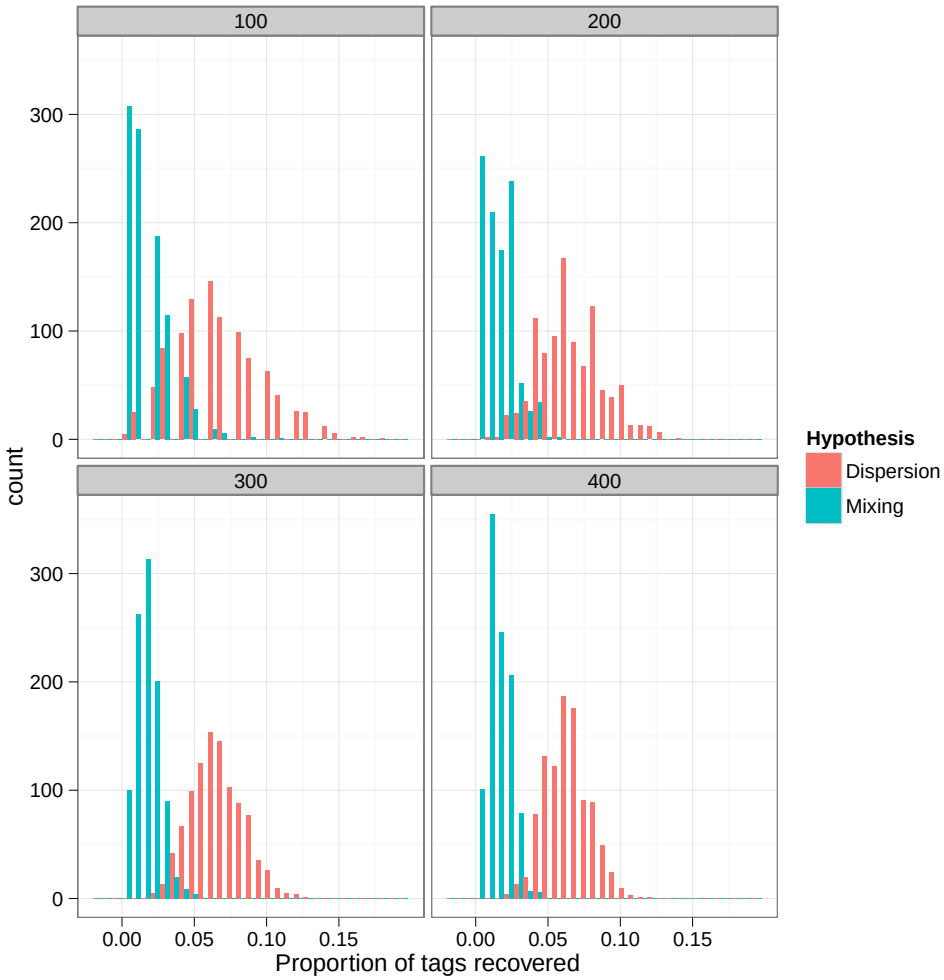

Figure 3: Histogram of the proportion of tags recovered in under the two different stock structure hypotheses faceted by the number of tags released.

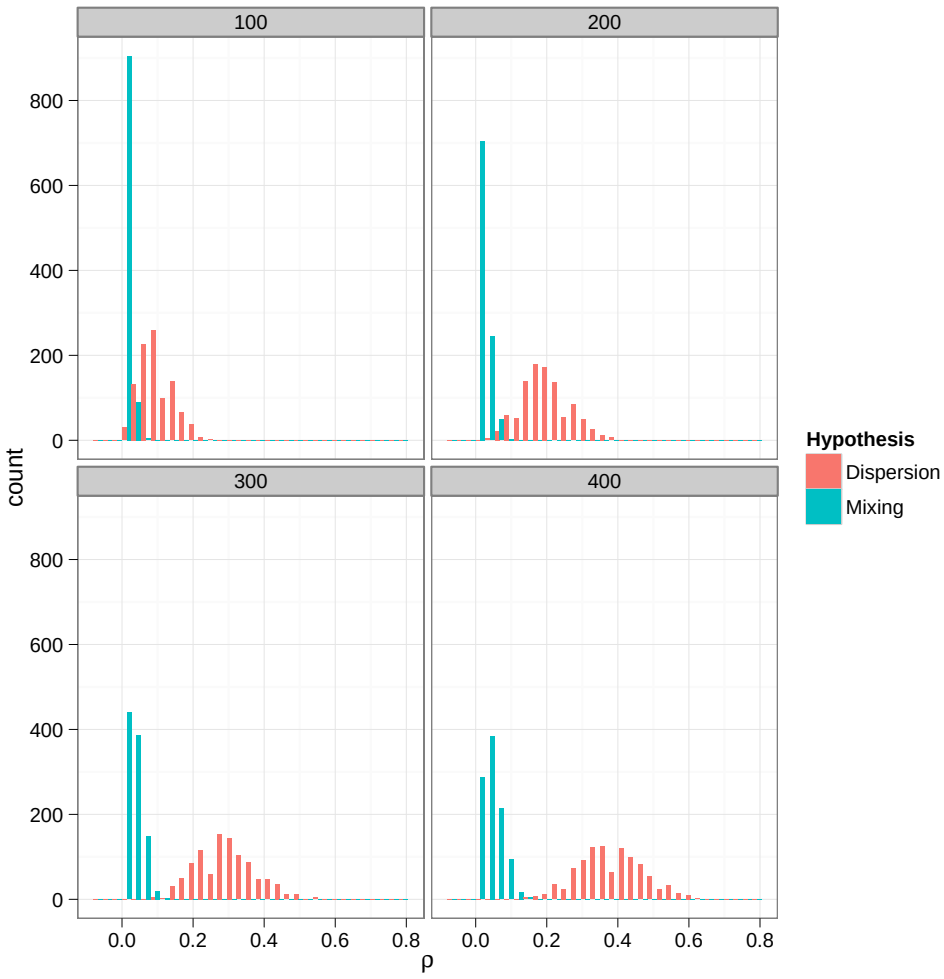

Figure 4: Histogram of the ratio of recovered tags to the number of genetic relations found in the catch under the two different stock structure hypotheses. The results are faceted by the number of tags released.

Table 1: The probability of rejecting H4 conditioned on the stock hypotheses using a direct tag-recapture experiment. The rejection interval was chosen such that the probability of type I error was either 5% or 10%.

Stock-	Number of tags							
Hypo.	100	200	300	400	500	600	700	800
H4	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10
H3	0.47	0.56	0.62	0.66	0.74	0.74	0.81	0.85
H4	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05
H3	0.40	0.48	0.49	0.54	0.64	0.62	0.72	0.75

	Number of tags						
	900	1000	1100	1200	1300	1400	1500
H4	0.10	0.10	0.10	0.10	0.10	0.10	0.10
H3	0.86	0.88	0.92	0.94	0.93	0.94	0.96
H4	0.05	0.05	0.05	0.05	0.05	0.05	0.05
H3	0.75	0.79	0.86	0.86	0.82	0.88	0.92

Table 2: The probability of rejecting H4 conditioned on the stock hypotheses using a genetic tag-recapture experiment based on number of recaptures (or captured relatives). The rejection interval was chosen such that the probability of type I error was 5%.

Stock	Effective number of tags				
hypo.	100	200	300	400	500
H3	0.740	0.915	0.982	0.988	0.999
H4	0.046	0.038	0.033	0.031	0.039

Table 3: The probability of rejecting H4 conditioned on the stock hypotheses using a genetic tag-recapture experiment based on ρ as defined by equation 10. The rejection interval was chosen such that the probability of type I error was 5%.

Stock	Effective number of tags				
hypo.	100	200	300	400	500
H4	0.05	0.05	0.05	0.05	0.05
H3	0.94	0.99	1.00	1.00	1.00