

Research programme on North Atlantic fin whales in relation to RMP Variant 2 and stock structure hypothesis IV.

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Abstract

This paper presents a proposal for a research programme on fin whales associated with RMP variant 2. The suggested programme follows the PRO_FORMA agreed by the SC in 2007 and incorporates research techniques suggested by the SC in this respect, s.a. genetic tagging, identification of close relatives and satellite tracking. A power analysis of the required sample size is included.

Introduction

At the conclusion of the two-year RMP implementation process on North Atlantic fin whales (*Balaenoptera physalus*) in 2009, the Scientific Committee agreed that RMP variant 2 could be accepted if accompanied with a research programme that it considered likely to resolve uncertainties around stock structure, in particular Hypothesis IV. This paper is prepared on request from the SC in line with the *PRO-FORMA* for research programmes associated with the 'variant with research' option, as agreed by the SC in 2007 (IWC 2008, Appendix 5 to Annex D: 115). This paper supersedes Gunnlaugsson and Víkingsson (2009).

The paper is organized according to the agreed PROFORMA as main text while the individual analyses are presented in Appendices.

Appendix 1 gives derivation of formulas for probabilities of relatives alive between samples collected at different times, both from catches and biopsies. Also available at <http://www.hafro.is/~thg/skaug/fin/probRelatAlive.doc>

Programs have been written to calculate parent-offspring and half-sibling/grand-parentage LOD score distributions with assumptions of no relatedness, parent-offspring or half-sibling/grand-parentage (Skaug 2001), from allele frequencies at a single locus, and the convolution of many loci. The probability of complete matching at a number of loci can also be calculated. These programs are available at <http://www.hafro.is/~thg/skaug/fin/>

The basis for abundance estimates for North Atlantic fin whales up to 2007 were reviewed in IWC (2009b). Some future work was identified, but none that would affect the application of the CLA to the WI and EG small areas. The estimates from NASS 2007 (Pike et al. 2008) were split on small areas in an earlier working paper that accidentally vanished and is therefore given again here.

Appendix 2 gives the allocation of the 2007 fin whale abundance estimates by blocks to small areas.

During statistical testing in preparation for this paper we found significant evidence from marking data to reject the hypothesis even without a research programme. This analysis will become a part of the research package presented here.

Appendix 3 gives this analysis of Discovery mark-recaptures by year after marking.

Appendix 4 discusses some general issues concerning Icelandic catch history.

Appendix 5 analyses the effect of different hypotheses on the ratio of recoveries from genetic tagging

in different small areas.

(1) Research objectives

In 2003, Iceland proposed that the SC started the process of a RMP *implementation* for North Atlantic fin whales (Vikingsson et al. 2003). Subsequently a *pre-implementation* was conducted during 2005-2006 (IWC, 2006a, 2007) according to a general scheme agreed by the SC in 2002 (IWC 2003). As a part of the pre-implementation assessment, a joint NAMMCO/IWC scientific workshop on the catch history, stock structure and abundance of North Atlantic fin whales was held in 2006 (IWC 2006b). The RMP *implementation* process was then formally initiated in 2007 following the 2-year time table agreed by the SC in 2004 (IWC 2005).

During the *pre-implementation* and the 1st intersessional workshop detailed discussions focused on the stock structure of fin whales in the North Atlantic. These resulted in seven stock structure hypotheses carried forward into the assessment process in the spirit of being inclusive.

At the 1st Annual Meeting the SC agreed unanimously that five of these (I, II, III, V, VI) should be assigned ‘high’ plausibility and hypothesis VII ‘medium’ plausibility. While there was some disagreement in the Committee regarding hypothesis IV (IWC 2009, p. 112), the SC agreed nevertheless to assign it high plausibility.

At the 2nd intersessional workshop the following six management variants were considered (SC/61/Rep3) (see Fig. 1):

- V1 Sub-area WI is a *Small Area*;
- V2 Sub-area (WI+EG) is a *Small Area*. The entire Catch Limit is taken in the WI sub-area;
- V3 Sub-area (WI+EG+EI/F) is a *Small Area*. All of the catch is taken in the WI sub-area;
- V4 Sub-area WI is a *Small Area*. Catch limits will be set based on survey estimates for the WI sub-area north of 60°N (both historic and future surveys). Note: trial NF15 is not applicable for this variant. The same proportions are used in setting future abundance estimates as for trial NF15 (see item F). The catch series is unchanged as all historic catches in the WI sub-area were taken north of 60°N;
- V5 Sub-areas WI and EG are taken to be *Small Areas* and sub-area WI+EG is taken to be a *Combination area*. The catch limits set for the EG *Small Area* are not taken;
- V6 Sub-areas WI, EI/F and EG are taken to be *Small Areas* and sub-area WI+EI/F+EG is taken to be a *Combination area*. The catch limits set for the EG & EI/F *Small Areas* are not taken.

Based on IST performance, all variants except V2 were classified as ‘acceptable without research’. Performance of V2 was ‘acceptable’ in all but one of the 27 ‘high’ weight trials, the exception (NF-10-2) being ranked as ‘borderline’ Three ‘medium’ weight trials were classified as ‘unacceptable’. All the four trials mentioned above are based on stock structure hypothesis IV. As variant 2 gives the highest catches (although considerably lower than the average for this operation) this is the variant preferred by the government of Iceland.

The process of designating the variant as ‘acceptable with research’ involves two steps:

- 1) To determine whether performance is acceptable if the variant is replaced by an ‘acceptable’ variant after an initial 10 year period.
- 2) To demonstrate to the SC’s satisfaction that a research programme has a good chance of being able to clarify the situation with respect to stock structure, and in particular to confirm or deny that stock structure hypothesis IV is implausible.

The SC has agreed that the requirements for stage 1 of the process have been met (IWC 2010)

The proposed research will therefore concentrate on evaluating the assumptions of Hypothesis IV, in particular how they relate to management variant 2. The objective here is to show that with proposed research there is a good chance of disproving the hypothesis or show that it should be modified such that performance becomes acceptable. This outcome must be shown to be unlikely if in fact the hypothesis is true.

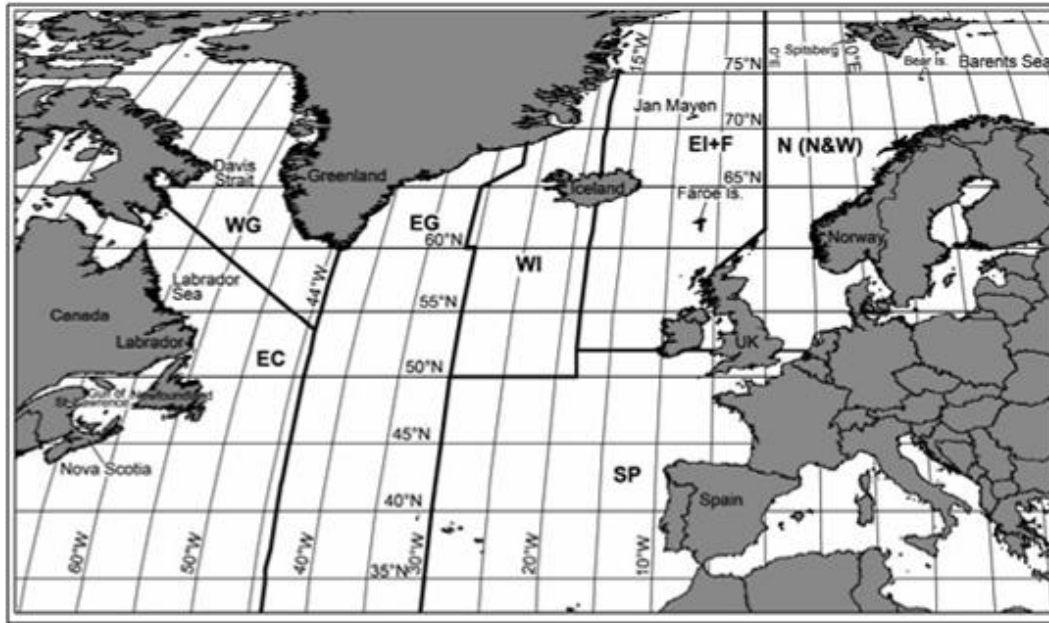


Figure 1. Map of the North Atlantic showing the fin whale Small Areas.

Basic features of hypothesis IV.

Hypothesis IV differs from the others hypotheses in that it assumes that there is no interchange between the three sub-stocks in the central North Atlantic at the breeding areas. The hypothesis assumes that the fin whales feeding west of Iceland (WI small area) are 90% of an isolated breeding sub-stock (C2) and 5% of each of separate breeding sub-stocks (C1 and C3) that feed mainly on each side of the WI area. Similarly 5% of the C2 breeding sub-stock goes to each side to feed. According to the hypothesis the visiting whales have no memory next year of where they were the year before and do not change their foraging behavior in response to changes in density of whales and/or prey in any one feeding area but will go back to their native feeding area 95% of the time next year.

For the hypothesis to hold, at most 5% of the whales from the neighbouring areas can be captured in the WI area in a single year (even if all the whales in WI were caught). This is how the hypothesis has been implemented in trials and how it should be tested. Different implementations of the hypothesis may be possible but would then call for trials to be rerun and should then be brought up at an implementation review. If more than 5% of the whales in one small area cross the area boundaries between seasons or within season the hypothesis must be considered disproved. If animals could be moving back and forth as long as they spend only 5% of the time in the wrong area, then more than 5% of the C1 and C3 breeding stocks could be captured in one season off WI. It would be impossible to disprove such a hypothesis with tagging. Such “visiting” behaviour would also be even less comprehensible as the density of whales falls in one area, and the “visiting” whales still spend only 5% of their time in that area having detected higher food availability (lower density) there.

As mentioned above hypothesis IV was accepted in spite of objections at the 2008 annual meeting, where points were raised by Gunnlaugsson (IWC, 2009). These included specific points regarding lack of fit to certain features in the available data and certain data that were not included in the IST model.

These points are covered under the research discussion below. More generally the two assumptions that set this hypothesis apart from other hypotheses are that of isolated breeding areas and no response in foraging behaviour to changes in density. Neither of these assumptions is based on any data. There is a lack of genetic structure in the North Atlantic (Pampoulie *et al.* 2008). Breeding sites are unknown, but the whales must be breeding in the deep waters in the open ocean with no geographic barriers. The history of the stock indicates that it recovered quickly in depleted areas. There are no references or data to support such permanently fixed proportional site fidelity in whale foraging behaviour. If the C2 breeding component would get exterminated then hypothesis IV predicts that 5% of breeding stocks C1 and C3 would continue to visit the area, but there would be no density response within the area such that it would ever come close to the original density. Such behaviour would have grave consequences for the species in case of anticipated environmental changes. We have called for a biological realizations of how this hypothesis is supposed to function but there has been no response. That in itself should have disqualified the hypothesis.

The SC has thus already chosen to ignore observations that contradict this hypothesis. In addition the SC has rejected that the decline in catch per boat in the early modern whaling period can be fitted in the IST model. In this case a 1% MSYR (of mature stock) would be rejected if this cpue trend were accepted. It is worth recalling that historical cpue series were the sole basis for most of the conservation actions recommended by the SC in the past. The SC however did not consider contemporary updates of cpue series to be reliable enough as a basis for the setting of quotas.. Although we consider that presently available data should be sufficient to refute assignment of high of “high plausibility” to stock structure hypothesis IV, we will still consider here the possibilities of contradicting the hypothesis with further research. Not considered here is meta research that would reduce the plausibility of the 1% MSYR case in general. Problems with sustainability only occur in case of assumed 1% MSYR (of the mature stock) for which there has been no agreement and is not consistently used in other work of the SC.

Research approaches

The plausibility of hypothesis IV could be resolved with research in mainly four ways, success with any one of which would suffice.

1) The assumption of an isolated breeding stock could be shown to be implausible.

If the animals from the feeding areas breed in overlapping areas they would be expected to interbreed. In light of the numerous cases of hybrids between fin and blue whales, how would animals with no genetic difference avoid interbreeding while breeding in the same area. If the animals inter-breed there will be no genetic stock to preserve and the 5%/90%/5% behaviour can not be genetically transmitted/sustained. Some statisticians at the 2nd Intersessional meeting still objected to this and stated that the 5%/90%/5% behaviour could be learned as the calves would follow their mothers to the feeding grounds. The calves are likely to follow their mothers only once but would have to learn different rules depending on which breeding grounds they came from. Such learning of proportions by animals is unheard of and hopefully not taken seriously by biologists in the SC. This approach would need direct observations (satellite tagging or other individual identification methods).

2) The assumed mixing proportion within the hypothesis could be statistically rejected

The only parameter in the hypothesis that can be statistically tested is the mixing. This could be done either with direct observations of movement of satellite tagged animals across the area-boundaries or through marking, direct or indirect (genetic relatedness).

3) Observations that do not confirm with hypothesis IV

Mixing might show signs of a time trend (this has already been found significant, see below). Significant mixing might be observed with areas outside the hypothesis.

4) Observations that need alterations or additions to hypothesis IV

Mixing might be shown to depend on sex or age or differ between direct markings (matches) and the different degrees of relatedness in genetic studies. The invariant behaviour of the animals with respect to density in the areas could be shown to fit inferior to biologically more plausible models. For instance the hypothesis could be assumed to hold in the initial equilibrium case but as density declines in one area the whales visiting that area would be more likely to revisit that area the next year. If the depletion level (D) in WI was high, the C1 (EG breeding stock) whales that visited the area last year would be more likely to come back there the following year, so instead of 95% of the visiting whales going back to EG, $(1-D)*95\%$ would do so. The results of incorporating different dynamics in the IST trials model could be compared by the fit in general to the data and qualitatively to the historical depletion of the stock observed in the early catches.

Research options

In 2006, the SC identified the following methods as having potential to distinguish among competing stock structure hypotheses (IWC 2007, p. 100):

- 1) New genetic methods based on analysis of close relatives.
- 2) Satellite tracking
- 3) Photo identification

Items 1) and 2) are captured below.

Robbins *et al* (2007) summarized the available photo-id catalogues in the North Atlantic and the Mediterranean Sea. The SC subsequently recommended that an effort be undertaken to match the small holdings in the eastern North Atlantic to catalogues in the western North Atlantic. To our knowledge this has not been undertaken yet. Given the relatively small size of the catalogues compared to estimated abundance of fin whales in the North Atlantic (50,000+) and that no catalogue exists for the main area of interest here, this option is not considered here further.

Genetic “mark-recapture” and relatedness studies

Previous genetic studies performed with microsatellite loci and mtDNA did not reveal any genetic structure among samples collected at several different feeding grounds over a period of 20 years (Pampoulie *et al.* 2008). Therefore, other analytical methods are needed to reveal potential dispersal between the areas. Mark-recapture genetic programs enable the unique identification of individuals by using hypervariable genetic markers. A genetic program based on “mark-recapture” analysis will prove more useful to assess potential exchange among the two entities targeted by the research proposal presented here (EG and WI), and to test hypothesis IV, than conventional population genetic analysis. A new method based on identification of close relatives (Skaug *et al.* 2008 and 2009) is particularly promising and most likely to provide significant data.

We start with a review of this NA fin whale relatedness study with special reference to this research program. Skaug *et al* (2009) report on relatedness within 358 samples that provide $n(n-1)/2=63,903$ distinct pairs from catches 1983-1989 in the WI area. Of the 22 likely related pairs detected there, 11 had possible parent-offspring (PO) relatedness and the rest a half-sibling/grand-parentage (HS) relatedness. The criterion for selection was a HS-LOD score (based on assumption of half-sibling/grand-parentage relatedness) (Marshall *et al.* 1998) of 6.7 or higher. We have calculated that this would have resulted in detection of 80% of the real PO pairs. An estimate provided of the likelihood of a false positive (FP) at the lowest HS-LOD score of the 11 possible PO pairs was 5%. A PO-LOD score (based on assumptions of parent offspring relatedness) was also provided, is more exact and the lowest PO-LOD score of the PO pairs was 11.3. The probability of an unrelated pair having a PO-LOD score of 11.3 or higher is $1.6e-6$, or 0.1 FP in a sample of this size. If the older animal in a pair was caught immature then both are immature and can not be a PO pair. The proportion immature in this operation was above 30% so the probability of both animals immature in a FP pair is around 0.1. In general, a minimum age difference is needed in a PO pair. With parameters from this operation about half of all FP pairs would be excluded as PO due to too little age difference. Age

readings were available for all the detected WI pairs and no discrepancies were found, the youngest parent, a female, having conceived at the age of 12 years. For comparison 6 of the 11 HS pairs are 6 years or less between.

The HS-LOD score of 6.7 or higher used as the criterion for detection in Skaug (2009) would only have detected 8% of the HS pairs in the WI catches. Of the 11 pairs detected 2.7 are expected to be unrelated false positives (FP). The true FP number must be higher due to other kinds of relatedness in the sample. About ¼ of the HS pairs were expected to be grand-parentage pairs. Based on age readings 9 of the 11 HS pairs can be excluded as grand-parentage related. The expected frequency of HS pairs in this sample is 1.2 times the number of PO pairs (assuming random reproductive success), but as the estimated detection is 80% for PO and 8% for HS pairs, the observed ratio HS/PO should be 0.12 but is $(11-2.7)/(11-0.05)=0.75$. This relative high frequency of HS pairs could imply that brood size is more varied or larger than expected or the number of FPs underestimated. Two of the detected HS pairs have complete matching at 10 out of the 15 loci which is highly unexpected out of just about $(11-2.7)/0.08$ or 100 true pairs (probability of HS complete matching at 10 or more loci $< 3/1,000,000$). This may imply more than a single lineage relatedness such as full sibling (probability of 10 full-matches is 1.5%), inbreeding, or errors, and needs further screening. With larger samples the FPs will mask the real HS pairs. More markers are then needed for inclusion of HS pairs and for higher detection rate and better precision.

Abundance estimation from relatedness studies

It is unlikely that new or more precise abundance estimates from surveys will change the trial results significantly, although it is assumed that such surveys continue as needed to provide input to the CLA. Abundance estimates will come as a by-product from relatedness studies and may prove to be useful. The Skaug (2009) study had 80% PO detection and 0.1 FP of which 50% would be rejected based on age readings. We have calculated the probability of a parent alive for a random PO pair in a stock with parameters in the range observed in the WI fishery (annual survival $S=0.9$, recruitment to fishery at ages 5 linear to 8 years) as 1.05. A simple mark-recapture estimate of the recruited stock based on the 11 PO pairs in this period is then $1.05 \cdot 0.8 \cdot 63,903 / (11 - 0.1 \cdot 0.5) = 4,902$ (cv 0.29 + components due to parent alive, detection, FP). The estimate for the 1+ population from surveys is given in Table 1. If all samples from this period could be worked up at triple the present number of loci it would likely result in about a hundred pairs that would provide an alternative abundance estimate of the recruited stock in this period, although likely downward biased due to related animals tending to occur in the same area (all samples are from the whaling grounds). In the same way a current local population estimate could be obtained from relatedness in ongoing catches with a lower cv than in surveys.

Detection of mixing over time from relatedness studies

According to hypothesis IV mixing does not change over time as the mixing in the WI area is assumed constant at 5% of the neighbouring breeding stocks. Markings in the other areas should be equally available from the start. In case of Discovery markings (without replacement) a slightly decreasing rate of returns with time is expected in the WI area, where in total 47 out of 191 got recovered, compared to the EG area where 9 out of 89 marks placed got recovered in the WI area. The mark returns however show greater differences over time, with 5 out of the 9 from the EG returned 5 years or later but only 4 out of the 47 (37 between season) from the WI area. Trials based on hypothesis IV fit the mark recoveries poorly and differ in that inherently they can not explain why marks placed on the grounds (WI) recover soon after marking (mean 2.7 years excluding same season recoveries) while marks placed in the EG area have recovered later (mean 5 years after marking although here including 1 same season recovery, $n=8$). During the SC discussions it was argued that the fit in these trials was no worse than in some other trials. This is not an issue since not all trials can reflect the true scenario. Hypotheses where there is gradual interchange/dispersal over time do predict the observed trend with time. The external recoveries are expected to increase with time and peak after some time (about 10 years when $S=0.93$ and dispersion is 7%). Due to the short time that elapsed from the placing of most of the Discovery marks till the cessation of whaling the data is limited and this time trend had not been tested statistically. In our considerations on sample size we however tested the Discovery data (see

appendix 3) and found a significant trend. These results are already sufficient to reject hypothesis IV. The proposed 100 biopsy samples from EG should double this dataset.

With a larger set of loci, a comparison of relatedness within and between the ongoing catches with the addition of the biopsies to the earlier (pre 1990) sampling might also show signs of mixing over time, incompatible with hypothesis IV. Over the period of 25-30 years there are still expected around two closely related individuals alive ($S=0.93$), so numbers might still turn out to be significant.

Detection of sex differences from relatedness studies

In the WI catches 9 animals Discovery marked outside the area have been found and identified to sex of which 7 were females. Relatedness studies could confirm such sex differences that are incompatible with hypothesis IV. The parent offspring pairs found in the relatedness study are 6 female-female pairs and only 3 male-male pairs. Such a difference is expected if daughters tend to stay closer to their mothers, than the sons. There are, however only two mixed sex pairs. They were determined from age readings as one father-daughter and one mother-son but these should both have had the same frequency as the above (3 to 6).

Mothers and fathers may only meet on the breeding grounds and not share feeding grounds. This would be incompatible with hypothesis IV which assumes isolated breeding stocks almost confined to separate feeding areas with just 5% random mixing per year.

Detection of relatedness to areas outside the frame of the hypothesis

Hypothesis IV can not explain the recovery of one mark recovered at West Iceland marked at Canada in 1979 as no interchange, direct or indirect, is assumed there between. This WI recovery from Canada was 9 years after marking and fits well in with gradual mixing between neighbouring areas. Possible HS pairs between areas were identified by Skaug (2009). One of these pairs has a complete matching at 12 loci out of 15 which is highly suspicious. A second pair had the lowest HS-LOD score (6.7). The third pair found in 13,832 pairs between Iceland and Norway had a HS-LOD score of 7.6 which gives a probability of 0.14 of a false positive. These cases need further screening. With additional genetic samples additional cases might be found in which case the hypothesis IV would have to be rejected.

Estimation of mixing across area boundaries from relatedness studies

Appendix 5 analyzes the ratio of recoveries from genetic tagging, biopsies in the EG area and within catches in the WI area, under different hypotheses. It is found that the proposed biopsy sampling of 100 whales in the EG area which should result in matches (direct plus relatedness recoveries) equivalent to around 500 markings, has a good chance of rejecting hypothesis IV.

Satellite tagging

Satellite tagging to reveal mixing between the areas

Satellite tagging early in the season could reveal animals moving across area boundaries within the season, and proportional time spent in each area. Two instances of such movements have been observed. One is a radio tagging experiment in 1980 (Watkins *et al.* 1984) where a whale was followed from west off Iceland to East Greenland in the course of a week. One Discovery mark placed at coastal East Greenland (of a total of 65 there) was found in the catch in Iceland a week later in 1986. As same season recoveries are generally not included in mark-recapture analysis, neither of these observations have been included in the IST model data and may not easily be incorporated there, but the likelihood of such events needs to be integrated with the likelihood of the model outcome. Mixing that exceeds 5% invalidates the hypothesis, and a binomial test with a proposed sample size of 50 animals (25 animals in the East Greenland and West Iceland area) would detect a difference between 5% and 20% with >80% power.

Satellite tagging to reveal overlap of WI and EG animals on the breeding grounds

Satellite tagging late in the season on the feeding grounds may survive long enough for detection of breeding grounds. The discovery of breeding grounds would then open up a range of research opportunities including genetic sampling and satellite tracking on breeding grounds.

(2) Methods – data collection

In 2009, Icelandic authorities set a 5 year quota of 150 fin whales per year. It is assumed that this will be the catch through out the 10 year research period. This catch level is about 2/3 of the average catches during the 1948-1985 commercial whaling period for which biological parameters have been estimated. If catches turn out to be lower then other effort such as biopsy sampling will need to be scaled up accordingly. At least 565 genetic samples exist from the pre 1990 whaling and 7 and 125 from 2006 and 2009 respectively. Problems have been encountered in work with some of these samples but we assume that most of the samples could be worked up within the research time-frame.

In relatedness studies the expected number of related pairs depends on the probability of the related animal being alive at the time of the re-sampling. This probability is highest if the sampling is spaced in time to a certain extent. If the time difference is one year the probability of a parent or grand parent alive in the earlier sample with offspring in the latter sample is higher by $1/S$ (S annual survival) and lower in the reverse case by S , but $1/S + S \geq 2$ for all S . The probability of a parent alive is highest when the time difference of samples is equal to the age at recruitment to the sampling (R), as animals are most likely sampled at that age and parents are certain to be alive (available) in the year when the animal was conceived (mating season taken as start of year). In the case when earlier samples are from catches, however, all samples (whales caught) prior to the birth of the later sampled animals are excluded as parents, so the probability becomes lower than in biopsy samples when the distance in time exceeds the minimum age of the later sampled animals. The implication is that not only will biopsies sampled at the start of the program be more likely to be matched directly in the catches, but also PO pairs will then be more likely.

If biopsy samples are collected prior to a 10 year sampling period the ratio of direct matches to relatedness matches changes from 2.8 in the first year to 5.5 in the last year ($S=0.93$) mainly due to fewer direct matches alive in the end.

Biopsies might be directed at recruited animals for immediate availability in the catches and for easier modelling.

Biopsies will be collected using ‘Larsen guns’ (Palsböll 2009)) and crossbows. Satellite transmitters will be instrumented using the ARTS system (Heide-Jørgensen *et al.* 2001, Víkingsson and Heide-Jørgensen 2005). Due to rapid technological development the choice of satellite transmitter will not be made until close to the start of the programme.

(3) Methods - analytical

An efficient two step relatedness study (Skaug 2010) for HS relatedness would need at least double the present number of loci to detect 35% of the HS pairs. With an anticipated total sample size of around 2,000 these would come along with around a hundred FP pairs in the first step that would then need to be further screened at additional markers in a second step. This would be realistic today. We anticipate that within a time-frame of 10 years the majority of HS pairs could be detected (double the present number of loci) with a tolerable FP error rate (1%).

Mother-foetus pairs do more accurately genetically mark the parental line in the population and should be integrated with the other pairs, although such samples will likely be few.

Direct genetic identification matches will be added to the Discovery marking data that is fitted in the trial model and relatedness data will be incorporated in a similar way in the models.

Models with modified hypothesis IV will be developed.

Methods to integrate different pieces of information that cannot be fitted in the IST model will be identified.

(4) Timeline – including assessment of feasibility

(a) Annual data collection – feasibility

Year 1. Feasibility study - Collect around 20 biopsies in EG small area and satellite tag 10 animals.

Year 2. Collect remaining biopsies in EG small area to fill 100 with effort allocation based on the feasibility study.

Year 2-10. Additional satellite tagging. Based on the feasibility study in year 1, 25 animals will be tagged in each of the two areas (EG+WI).

Years 1-10. Collect samples from catches.

(b) Annual laboratory work – data validation.

Years 1-6. Identify new markers for relatedness studies.

Years 6-10. Genetic work on all samples with a minimum of the equivalent of triple the number of present loci.

(c) Annual analysis and completion targets.

Years 1-6 Programming and development of models.

Years 7-10 Statistical analyses of samples and model runs.

Work on the IST model amendments and modified hypotheses will need to be in cooperation with the Secretariat Computing. The work will take note of any best practice guidelines or requirements established by the Committee.

(a) Data availability: Data will be made available to SC members as specified under the DAA.

(b) Reports to the SC: Progress will be reported to the SC annually.

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Table 1. WI total abundance (N) and C.V.

Year	Abundance (N)	C.V.
1988	4,243	0.229
1995	6,800	0.218
2001	6,565	0.194
2007	8,118	0.26

Appendix 1. Recapture probabilities in relatedness studies

Probability that an animal is alive between samples spaced d years apart.

Assume annual survival rate of recruited animals is S . Given an animal from the earlier sample the probability of the animal being alive in the later sample after d years has decreased to S^d . For samples of size n_1 and n_2 the number of matching trials between samples is $n_1 \cdot n_2$. If samples can be assumed to be sufficiently (e.g. either one fully) random or sufficient mixing between sampling, the expected number of matches between samples, that are d years apart, where N is total population size, is

$$S^d n_1 \cdot n_2 / N$$

Probability that a single older half-sibling is alive.

Denote the age of the younger sibling by $i+R$ and consider a fixed age difference $k>0$ so the age of the older sibling is $i+k+R$ at the time of sampling, where R is knife-edge recruitment age. As the maturity age R cancels out in the following formulation it can be omitted. The probability of the younger sibling being at age i is $S^i (1-S)$ for all $i \geq 0$. Probability of the older sibling being alive is then S^{i+k} as it has to have survived this period. The probability that the younger sibling is at age i and the older sibling is alive is $S^{i+k} S^i (1-S)$. The probability of the younger sibling being at any age and the older sibling alive is $\sum S^{i+k} S^i (1-S)$ over all $i \geq 0$ is $S^k / (1+S)$.

The probability of an age difference k decreases by S^k as parent is more likely to be dead as time passes, but as it must sum to 1 the resulting probability is $S^{k-1} (1-S)$.

The probability of an older sibling being alive weighted over all $k>0$ is $\sum S^{k-1} (1-S) S^k / (1+S)$ or

$$S / (1+S)^2$$

When $S=0.9$ the above gives a probability of 0.23 but as each pair provides for two trials the expected number of matches is 0.46 for a pair. The number of distinct pairs in a sample of size n is $n(n-1)/2$. The expected number of half-siblings is two (one maternal and one paternal) so one sibling is expected to be older. With exactly one older half-sibling the expected matches are $0.46 n(n-1) / (2N)$. If reproduction is however assumed random with on average two offspring (*Poisson*, $m=2$) the average number of older siblings is 2 ($=m^2/2$). If some individuals are inherently more successful in reproduction this number will be higher. The assumption here is that siblings are born in different years but many paternal siblings could be born in the same year, which makes the probability for paternal siblings slightly higher. The same applies in case of gradual recruitment over a few years but over many years the effect will be negative. Similarly, for fin whales maternal siblings are less likely in consecutive years, which makes the probability for maternal siblings slightly lower.

Probability older half-sibling is alive between samples spaced d years apart.

For an animal from the earlier sample the probability of the older sibling being alive in the later sample decreases by S^{-d} and given the expression above it becomes

$$S^{d+1} / (1+S)^2$$

Given an animal from the later sample consider the probability of the sibling being alive in an earlier sample. For a fixed age difference $k \geq d$ the probability that the older sibling is alive is higher by S^{-d} or S^{i+k-d} . The probability of the younger sibling being at any age and the older sibling being alive is $\sum S^{i+k-d} S^i (1-S)$ and for all $i \geq 0$ this is $S^{k-d} / (1+S)$.

For a fixed age difference $k < d$ the older sibling may not be born or recruited. The probability of the younger sibling being at any age and that the older sibling is available is $\sum S^{i+k-d} S^i (1-S)$ over all $i \geq d-k$ is $S^{d-k} / (1+S)$. Weighted with probability that age difference is k is therefore $\sum S^{k-1} (1-S) S^{d-k} / (1+S)$ or $\sum S^{k-1} (1-S) S^{k-d} / (1+S)$ for $k \geq d$ + $\sum S^{k-1} (1-S) S^{d-k} / (1+S)$ for $k < d$ is $S^{d-1} / (1+S)^2$ + $S^{d-1} (d-1) (1-S) / (1+S)$ is

$$S^{d-1}(S^2+d(1-S^2))/(1+S)^2$$

For samples of size n_1 and n_2 the number of distinct matching trials between samples, for each animal in the earlier sample looking for the older sibling in the later sample, and the reverse is in both cases $n_1 \cdot n_2$. The sum both ways is $S^{d+1}/(1+S)^2 + S^{d-1}/(1+S)^2 + S^{d-1}(d-1)(1-S)/(1+S)$. The probability of an older sibling being alive is then

$$S^{d-1}(2S^2+d(1-S^2))/(1+S)^2$$

When $S=0.9$ the maximum is attained for d around 1 when the sum of the probabilities of the older sibling being alive either way is 0.501. Expected matches are then $0.501 \cdot n_1 \cdot n_2 / N$. When d is 9 the sum of the probabilities is still 0.374. These calculations are for exactly one older sibling. With random variation in brood size this number is 2 (see above).

The probability that the parent is alive between samples spaced d years apart.

When d is 0 the probability with knife edge recruitment R is $S^R/(1+S)$. For larger d the probability of the parent being alive in a later sample decreases by S^d and is therefore

$$S^{R+d}/(1+S)$$

Given an animal from a later sample the probability of the parent being available in the earlier sample is

$$S^{R-d}/(1+S) \text{ when } d \leq R$$

When $d \geq R$ and the earlier sample is lethal, a sampled animal may be excluded as the parent (or grandparent) and a rewording is in order as: proportion of animals at time of later sampling with the specified unique ancestry possible in the earlier sample and is

$$S^{d-R}/(1+S) \text{ when } d \geq R \text{ and earlier sample is lethal.}$$

When the earlier sampling was non-lethal and R equals B , the age at first parturition, this is

$$S^{d-R}(1/(1+S) + (d-R)(1-S)) \text{ when } d \geq B=R$$

When earlier sampling was non-lethal and $B > R$

$$(1+S(1-S^{d-R}))/((1+S) \text{ when } B \geq d \geq R \\ S^{d-B}(S^{B-R}/(1+S) + (d-B)(1-S) + 1-S^{B-R}) \text{ when } d \geq B$$

Each animal has exactly two parents so expected matches are $2 \cdot n_1 \cdot n_2 / N$ times the sum of the probabilities both ways. When $S=0.9$ the probability is highest when $B \leq d < B+1$. If recruitment is assumed 20, 40, 60, 80 % by year the probability within sample is higher by 3% compared to a knife-edge recruitment (at the age of 50% recruitment + 0.5) but this difference will be less if samples are spaced R years apart.

The probability that the grandparent is alive between samples spaced d years apart.

The grandparent must have been alive at the birth of its child which is the parent of the grandchild. With knife-edge recruitment R and age at first parturition B , denote the age of the parent/child $R+B+k$ ($k \geq 0$) at the sampling of the grandchild. The probability of the age of the grandchild $R+i$ is $S^i(1-S)$ and being born at the age of parent $k-i$ is $S^{k-i}(1-S)$.

Summing over all i ($k \geq i \geq 0$) gives $(1-S)^2 S^k(k+1)$ and when $d \leq R+B$ the probability of the grandparent alive is $S^{R+B+k-d}$. Summing over all $k \geq 0$ when d is 0 the probability of the grandparent alive is $S^{R+B}/(1+S)^2$. Given an animal in the earlier sample the probability of the grandparent being alive in a later sample decreases with d by S^d and is

$$S^{R+B+d}/(1+S)^2$$

Given an animal from a later sample the probability of the grandparent present in the earlier sample is

$$S^{R+B-d}/(1+S)^2 \text{ when } d \leq R+B \\ S^{d-R-B}(1+(d-R-B)(1-S^2))/(1+S)^2 \text{ when } d \geq R+B \text{ and earlier sample is lethal } (k \geq d-R-B)$$

For $S=0.9$ the matching of a grandparent in the earlier sample to a grand child in a later sample is highest when the probability of a grandparent present is 0.32 as d is 4 to 5 years greater than $R+B$. With exactly 4 grandparents expected matches in $n_1 \cdot n_2$ trials are then $1.28 n_1 \cdot n_2 / N$ (when $R+B$ are in the range for baleen whales the matches then the other way are negligible).

Appendix 2

NASS-2007 fin whale abundance estimates by blocks as allocated to small areas

The estimates from NASS 2007 (Pike et al. 2008) by survey blocks (b) used were based on high and medium confidence sightings only with no correction for $g(0)$ or distance estimation bias.

Proportions ($P_{i,b}$) of survey block estimates to allocate to each small area (i) East-Greenland (EG), West Iceland (WI) and East Isl. Faeroes (EIF) were calculated based on:

Area (A_i) (in Nautical Miles), number of animals sighted ($S_{i,b}$) and effort ($E_{i,b}$) in Nautical Miles surveyed in Beaufort <5 .

Survey Block	Vessel Code	Proportion in			$A_i S_{i,b} / E_{i,b}$
		EG	WI	EIF	
FE	F	-	-	1	
FS	F	-	0	1	
FX	F	-	0	0	
IN	V	-	0.41	0.59	$23535 \cdot 6 / 171, 72232 \cdot 9 / 552$
NW	V	0.60	0.40	-	Sighted animals 6, 4
RN	A	0.77	0.23	-	$84993 \cdot 203 / 785, 40461 \cdot 101 / 638$
RS	A	0.94	0.06	-	$87139 \cdot 32 / 601, 5318 \cdot 1 / 17$
SC	J	0.09	0.91	0	$62588 \cdot 6 / 630, 134479 \cdot 85 / 1863$
Total N_i		12214.5	8117.9	1612.5	
CV_i		0.20	0.26	0.26	

In block NW surveyed by Venus (V) sea-ice limited effort. There is a question as to what the area is due to ice cover, so here just the proportion of animals sighted in each component is used.

For a Small Area with total estimate N_i the CV_i was calculated by summing over all survey block components in the area:

$$CV_i^2 = 1/N_i^2 \sum_b (CV_b \cdot N_b)^2 P_{i,b}$$

Appendix 3 Test for time trend in (Discovery) mark returns from EG small area

The data used is given in table 1, recoveries by year after marking for up to 10 years (longest recovery) in WI and EG small areas (Gunnlaugsson and Víkingsson 2008). A few markings in the IEF small area with no recovery were left out.. The model tested is

$$r_{d,a}/n_{d,a} \sim S_a^d/N_a$$

where d is the years since marking and a is area (WI, EG). $r_{d,a}$ is the number of recoveries d years after marking in the area. $n_{d,a}$ is the sum of observations d years after marking or catch times remaining marks ($c \cdot m$) over all marking experiments. S is annual natural survival not including fishing, since that is accounted for by updating the remaining marks with recoveries. According to hypothesis IV the S (the estimate of the coefficient with d) should be the same in both areas. A Binomial Logit model with weight n was tested in the R package and the interaction $a \cdot d$ was found significant with a value of 0.015. A one sided test would be natural here, giving half this value. The estimate of S in the EG area was >1 implying increasing availability of marks from there over this period. Analyses of Discovery markings have been considered unreliable due to problematic factors. These are possible misjudgement of mark success, mark mortality, initial mark loss, mark shedding and lack of returns, all of which should lead to fewer mark-recoveries. It is therefore noticeable that the recoveries from the Discovery markings are initially higher, as seen by a lower simple mark-recapture estimate of around 3,000 based on 1-3 year returns (Gunnlaugsson and Sigurjónsson 1989), than those observed from the relatedness samples in the same period (see above). The problematic factors should not affect differently the recovery rate from the areas, except when updating the remaining marks by subtracting recoveries, there could be increasingly too many marks assumed in the external area, where recoveries were few. We tested for the sensitivity to this by preparing another table where markings were reduced initially by 20% but found this to have a negligible effect on the interaction.

For external areas a model with dispersion would be

$$r_{d,a}/n_{d,a} \sim S^d(1-F_a^d)/N_a$$

where F_a is fidelity to that area. With $S=0.93$ and dispersion 7% ($F_{EG}=0.93$) the peak in recoveries is in 10 years. This model is not log-linear and has different parameters and so is not directly comparable to the model above. This model would have difficulty explaining the short term movements observed between the areas. The reality is most likely in between these two where the animals forage into new territory but do not persist there unless they happen to find more food in that instance. The exact model is not of fundamental importance as long as the isolation assumed in hypothesis IV is rejected.

Table 1. Discovery mark returns (r) and the catch times marks remaining ($c \cdot m$) summed over all marking experiments and given by year after marking (d) and by small areas.

Area:	WI		EG	
d	$c \cdot m$	r	$c \cdot m$	r
1	35243	12	18337	1
2	30316	9	14426	1
3	26221	6	13853	0
4	20741	6	12797	2
5	16862	0	11273	1
6	15401	1	9340	0
7	12171	2	8408	0
8	9496	1	8514	1
9	5792	0	5186	1
10	5128	0	4688	1

Appendix 4 General issues concerning Icelandic catch history

Modern whaling started west of Iceland in 1883 and closed in 1915 due to a ban on whaling in Iceland imposed by Icelandic authorities (Sigurjónsson 1988). The operation started by concentrating on blue whales and later humpback whales although fin whales were by then hunted also in considerable numbers. Fin whales comprised about half the total catch (roughly 8,000 fin whales) but in the last years around 80% of the catch and the remainder by then partly sei whales (fig 1). By 1893 the catch was up to 495 and the peak was in 1901 with 1,019 whales caught west of Iceland, when stations started closing down and moved to the East coast. Catches stabilised west of Iceland at around 200 in the period 1905 to 1911. In the last year 52 whales were caught. When the stations moved to the East coast the whalers complained that whales were few and small of the west coast. Catches collapsed quickly at the east coast. The operation thus spanned 43 years and the fin whales being the last major stock to be targeted had all that time to take advantage of the reduced competition by the other species. The stocks of blue and humpback whales were certainly still severely reduced at the start of the more recent operation in 1948, when they were rarely seen, but fin whale catches were then again good so there must still have been a considerable number of young fin whales left in 1915. The latter operation took on average 234 fin whales per year up to 1985. Due to species interaction the total catch of fin whales may therefore by far have exceeded what can realistically be explained in a single species model. The humpback and blue whales around Iceland have been increasing in recent years (Sigurjónsson and Gunnlaugsson 1990; Gunnlaugsson et al 2004; Pike et al. 2009). A single species model hitting recent estimates of around 20,000 fin whales (Pike and Gunnlaugsson 2006; Pike et al. 2008, Víkingsson et al 2009), will have to start from a very large initial stock to explain these large cumulated catches, especially if a low MSYR is assumed, and so the stock will always appear to be severely depleted in that comparison. This may be a similar situation to that in the Southern Ocean where the large catches of fin whales may need to take into account the reduced competition by the stocks depleted first, and thereafter the demise of fin whales, the minke whale there may also have responded similarly (Mori and Butterworth 2003).

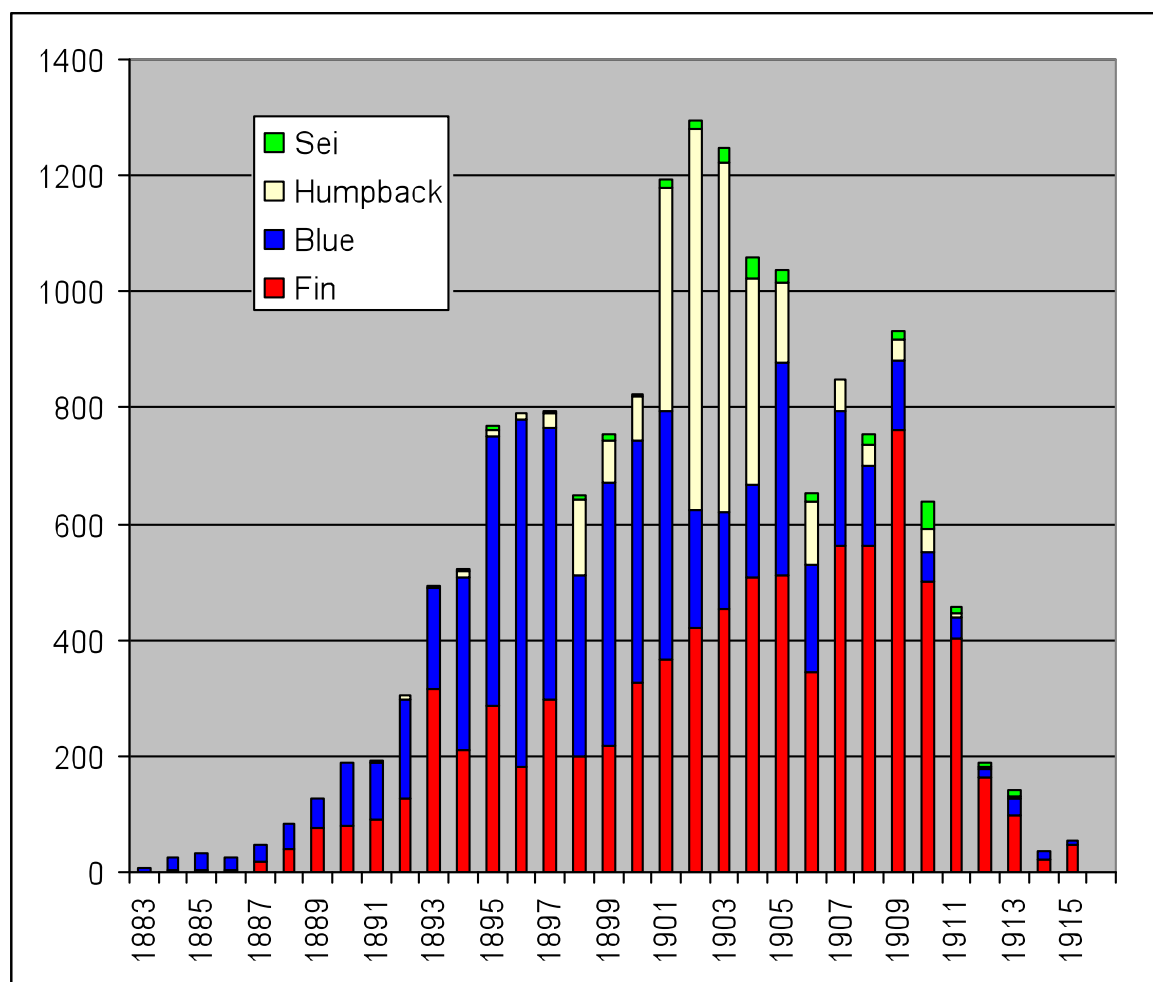


Figure 1: Prorated historical landings of large whales in Iceland 1883-1915.

Estimation of mixing across area boundaries from relatedness studies

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Abstract

The prominent feature of stock hypothesis IV for North-Atlantic fin whale is that three completely separate breeding substocks inhabit and mix in the East-Greenland (EG), West-Iceland (WI) and East-Iceland (EI) sub-areas with little or no overlap between the breeding areas. Furthermore, the mixing between the three areas is considered to be low. Here we will present a tag-recapture simulation to compare hypothesis IV with three alternative stock migration hypotheses.

The model

In this discussion we will assume that the sub-areas close to Iceland, i.e. EG, WI and EI, are occupied by three distinct breeding stocks, C_1 , C_2 and C_3 . Furthermore it is assumed that a large majority of each sub-stock occupies only one area. Migrations between EG, WI and EI are only considered to take place annually, that is when a whale has migrated from its breeding grounds to one of the sub-areas it stays there until it migrates back to the breeding ground. We wish to simulate a 10 year stock migration with a whaling operation. The Icelandic whaling operation is solely based in the WI subarea with an annual quota of 150 animals. Additionally a (DNA or direct) tagging experiment is conducted in the EG sub-area at the beginning of the 10 year period.

We assume that the annual migrations for each whale follows an i.i.d. Bernoulli process where the parameter of the distribution is stock and area dependent. We consider two possible migration patterns:

- Hypothesis IV: A whale, that belongs to sub stock C_i , returns to its stocks home area with probability $1 - p_{A,i}$ and migrates to other areas with probability $p_{A,i}$. Furthermore a whale in sub stock C_2 , with a home area WI, is equally likely to migrate to EG or EI small areas while whales in other sub stocks can only migrate to their home areas or the WI small area.
- Dispersion: A whale returns to the same area as last year with probability $1 - p_{B,a}$ and migrates to other areas with probability $p_{B,a}$, where a denotes one of the small areas EG, WI and EI. Furthermore a whale in small area WI can migrate to EG or EI with equal probability or migrate back, while whales in the other small areas can only migrate to the same area or WI.

Additionally the probabilities $p_{A,i}$ and $p_{B,a}$ are density dependent, where the number of whales within each small area can not exceed 5000 whales for small areas EI and WI and 15000 whales for EG.

Whaling and tagging is also considered to follow an independent Bernoulli distribution where the parameters are adjusted in order for the expected number of successes to be the quota in the WI and number of tags in EG respectively.

In all we will consider 4 stock hypotheses, two hypotheses for each migration pattern where we vary the mixing between the areas:

- Hypothesis IV:

5% (Unaltered hypothesis IV) We assume here that the maximum migration probability, $p_{A,i}$, is 5% for C_1 and C_3 while it is 10% for C_2 , that is 5% for EG and EI.

20% (Augmented hypothesis IV) We assume here that the maximum migration probability, $p_{A,i}$, is 20% for C_1 and C_3 while it is 40% for C_2 , that is 20% for EG and EI.

- Dispersion:

5% We assume here that the maximum migration probability, $p_{B,a}$, is 5% for EG and EI while it is 10% for WI.

7% We assume here that the maximum migration probability, $p_{B,a}$, is 7% for EG and EI while it is 14% for WI.

For all hypothesis we simulated each hypothesis with 500 tagged whales and for all different scenarios the simulation was repeated 100 times. Additionally natural mortality was assumed to be 0.95. The number of caught tagged whales was compared with the number of pairs in the catch by calculating the ratio

$$\rho = \frac{\sum_{i \in \mathfrak{C}} T_i}{\sum_{i \in \mathfrak{C}} R_i} \quad (1)$$

where \mathfrak{C} denotes the different sub stocks, C_1 , C_2 and C_3 , T_i is number of tagged whales of the sub stock i that are caught in the WI small area and R_i is the number of the relatedness detected in the catch which is expected to be:

$$R_i = \frac{c_i(c_i - 1)}{2n_i}$$

where we consider only one relatedness per individual, c_i is the total catch and n_i is the total size of sub stock i .

Results

In figure 2 and table 1 we can see the results from the simulation study with 500 tags and 100 iterations for each hypothesis. Note from figure 2 that the variance of ρ under A1 is smaller than for the other three hypotheses. Also we can reasonably distinguish between hypothesis A1 and the other three hypotheses as ρ under the hypotheses A2, B1 and B2 is larger than the 95% quantile of the distribution of ρ under A1 for more than 80% of the simulated ρ -s. In figure 3 we see the proportion of tagged whales as a function of years and the four different hypotheses. The proportion under hypothesis IV 5% and 20% are essentially constant with respect to time while the dispersion hypotheses exhibit a much greater time trend. The slight linear effect for hypothesis IV 5% and 20% can be explained by stochasticity.

Quantile	A1	A2	B1	B2
5%	0.00491	0.01977	0.01205	0.02058
10%	0.00649	0.02335	0.01496	0.02336
50%	0.01135	0.03322	0.02435	0.03171
90%	0.01576	0.04605	0.03257	0.04361
95%	0.01715	0.04691	0.03863	0.04638
$\#\{\rho > q_{90\%}\}$	10	100	86	100
$\#\{\rho > q_{95\%}\}$	5	98	83	100

Table 1: The upper table shows the quantiles of the distribution of ρ under the four hypotheses. The lower table shows the number of ρ -s larger than the upper 90% and 95% quantiles for hypothesis A1 (hypothesis IV).

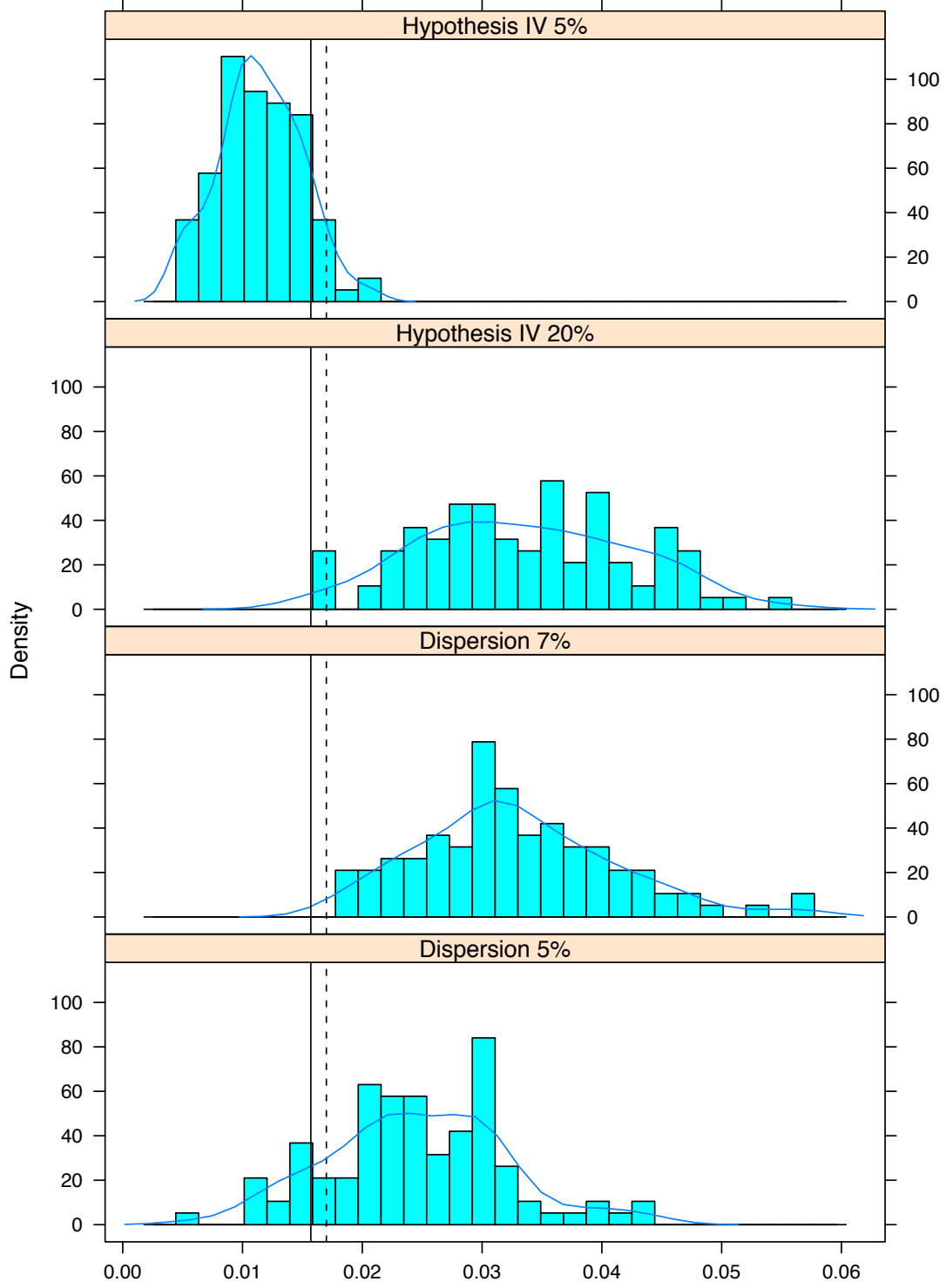


Figure 1: A histogram of ρ simulated under the four different hypotheses. The solid and broken lines represent the 90% and 95% quantiles for pattern A1 (hypothesis IV). The number of tags in this simulation was 500.

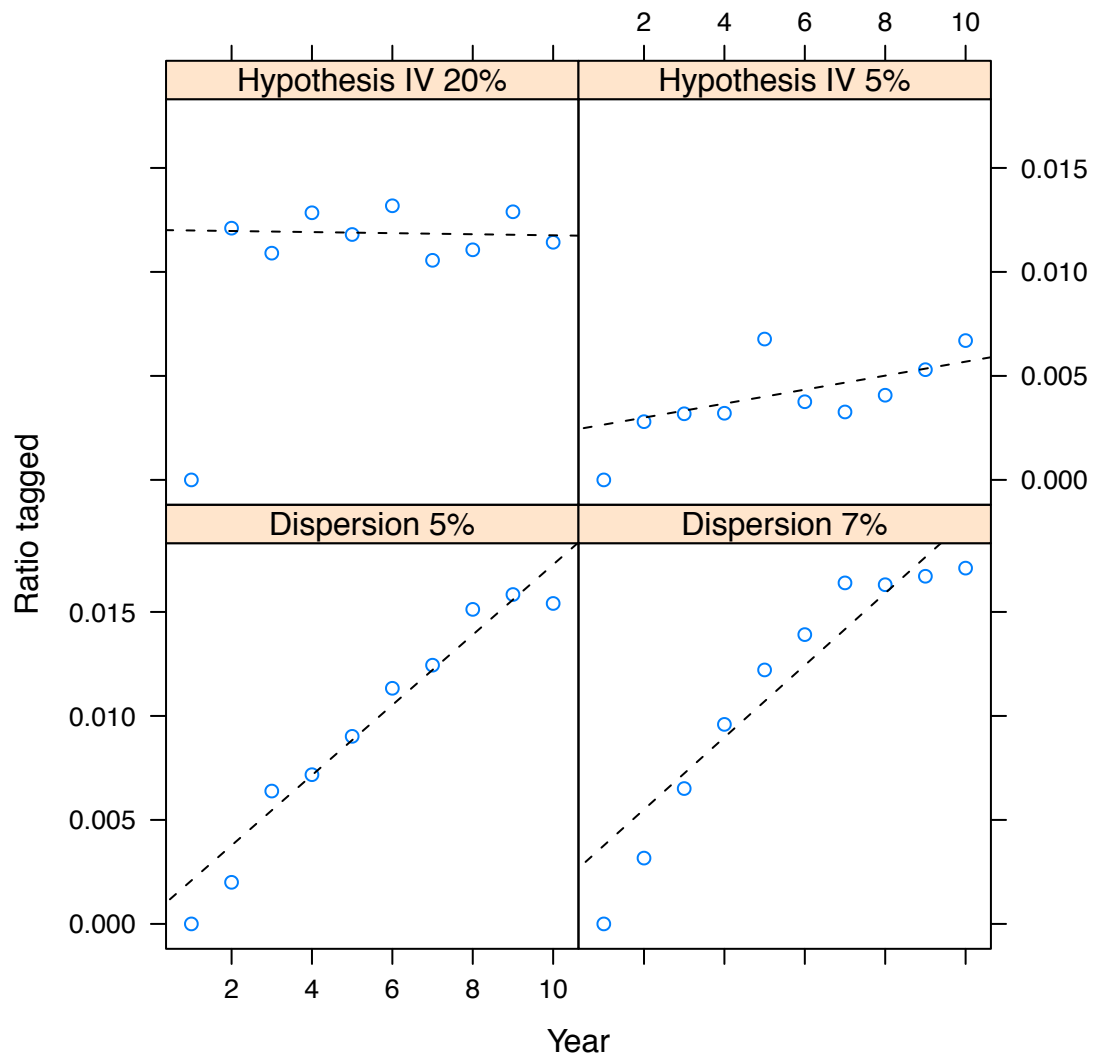


Figure 2: Proportion of tagged whales in the WI sub-area as a function of year under the different hypotheses, one simulation each.