

Review on the genetic stock structure of North Atlantic fin whales (*Balaenoptera physalus*): Past, present and future.

CHRISTOPHE PAMPOULIE AND ANNA KRISTÍN DANÍELSDÓTTIR[§]

Marine Research Institute, Skúlagata 4, IS-101 Reykjavík, Iceland

[§]Present address: Matís Ltd., Vinlandsleið 12, IS-113 Reykjavík, Iceland

ABSTRACT

Genetic structure of North Atlantic fin whale *Balaenoptera physalus* has now been studied for many years, from the early ages of allozymes to the most recently developed genetic techniques such as mtDNA and microsatellite loci, and even gene sequencing. Here in an attempt to clarify our general knowledge on the stock structure of this species, we summarized the results of the different genetic markers used to describe the stock structure of North Atlantic fin whale within and between IWC stock boundaries.

KEYWORDS: BALAENOPTERA PHYSALUS, NORTH ATLANTIC OCEAN, GENETICS, MIGRATION, ALLOZYMES, MICROSATELLITE LOCI, MTDNA.

INTRODUCTION

The North Atlantic fin whales are known to undertake long, annual migrations between high-latitude summer feeding areas and low-latitude winter breeding areas like most of the baleen whales. The details of these migrations including the locations of wintering areas are however poorly known. Little is also known about the genetic composition and biological characteristics of the group of individuals located at feeding grounds. So far, the geographical delineation of fin whale stocks in the North Atlantic Ocean is not well established, although it is believed that several distinct stocks of the species inhabit the North Atlantic Ocean. In the mid 1970's, the International Whaling Commission (IWC) divides the North Atlantic fin whales into seven management stocks (Donovan, 1991):

- 1) the British Isles, Spain and Portugal
- 2) North Norway and the Arctic Eastern North Atlantic
- 3) West Norway and the Faroe Islands
- 4) East Greenland and West Iceland
- 5) West Greenland
- 6) Newfoundland and Labrador
- 7) Nova Scotia

This division was originally based on various methods including catch data, occurrence and length distributions. Later on, morphological studies (Jover, 1987, 1991), mark-recapture data (Gunnlaugsson and Sigurjónsson, 1989; Sigurjónsson *et al.*, 1991) and analysis of genetic markers (Árnason and Jónsdóttir, 1988; Daníelsdóttir *et al.*, 1991) supported the discrimination of these different areas (see Figure 1 for the actual management areas).

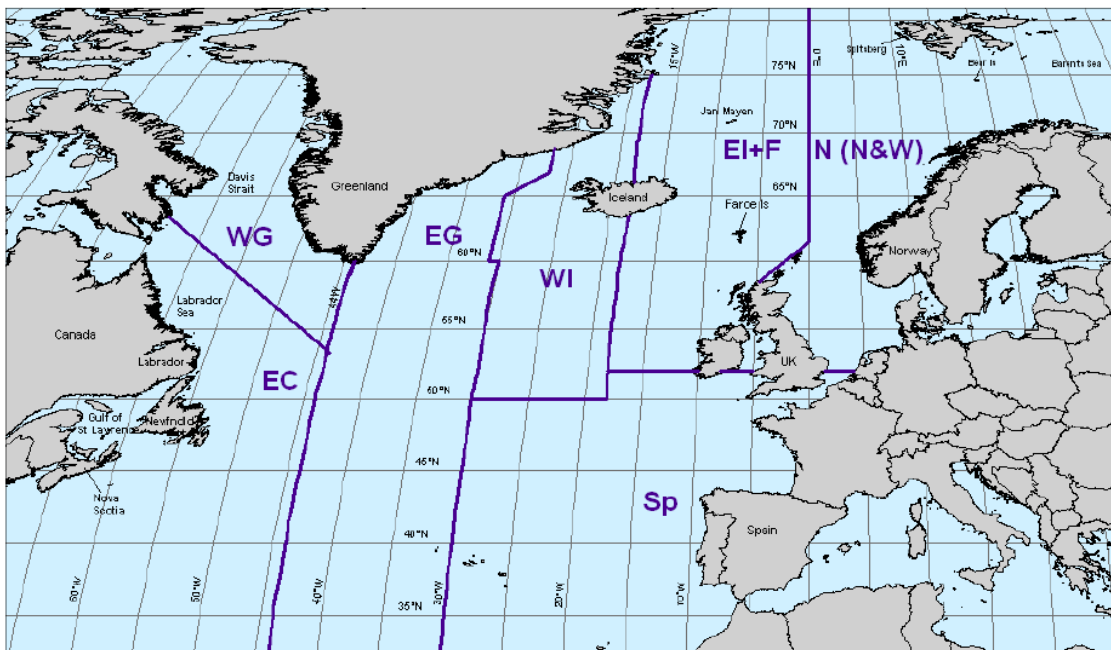


Figure 1. Map showing the seven management areas considered by the IWC (SC/60/Rep3).

Population genetic studies have been carried out on the North Atlantic fin whale stocks at the early ages of genetics, using allozymes (Daníelsdóttir *et al.*, 1992; Daníelsdóttir, 1994) and more recently using microsatellite loci and mtDNA (Bérubé *et al.*, 1998; Palsbøll *et al.*, 2004; Daníelsdóttir *et al.*, 2005, 2006; Bérubé *et al.*, 2006; Skaug *et al.*, 2006; Pampoulie *et al.*, 2008, 2013). Some genetic studies have revealed significant divergence among some fin whale stocks in the North Atlantic which were 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; Sigurjónsson and Gunnlaugsson, 1985; Gunnlaugsson and Sigurjónsson, 1989; Sigurjónsson *et al.*, 1991; Víkingsson and Gunnlaugsson, 2006), while others have been revealing a lack of

genetic structure among samples collected in different IWC stocks boundaries (Pampoulie *et al.*, 2008). In addition, Arnason (1981) suggested that the occurrence of genetically distinct fin whale stocks is unlikely within a limited area and that no solid evidence has been reported in favour of the existence of several fin whale stocks in the Northeastern Atlantic. In an attempt to clarify our general knowledge on the stock structure of this species, we summarized the results of the different genetic markers used to describe the stock structure of North Atlantic fin whale within and between IWC stock boundaries.

SUMMARY OF THE MAIN RESULTS

The results of the different genetic approaches performed on the North Atlantic fin whale are summarized in Table 1. Below, we summarized the recent approaches which might be relevant to the IWC in the absence of clear pattern from common genetic approaches and the observed general low levels of differentiation at feeding grounds.

RESULTS RELEVANT FOR FUTURE INVESTIGATION

Estimation of number and migrants and gene flow

Bérubé *et al.* (2006) provided information on migration rates among areas of North Atlantic using nuclear and mtDNA loci. The authors noted that while allele or haplotype frequencies may be statistically different among sampling areas, the observed level of genetic differentiation was very low. They therefore concluded that the most relevant and meaningful measure based on genetic data may be the current migration rates which they estimated using BayesAss. Their analysis revealed that 20 percent or more of individuals in a single area seemed to be immigrants. They stated that such exchange rates will typically lead to demographically correlated populations in the geographical areas investigated, which should therefore not be viewed as demographically or genetically independent populations. In addition, this was supported by the number of migrants estimated from the F_{ST} estimates which was on the order of 30 migrants per generation.

Relatedness analyses

Skaug *et al.* (2006) presented relatedness analysis based on a dataset consisting of 15 microsatellite loci from 226 fin whales from the North Atlantic which were screened for related individuals. Five pairs of individuals meet their criterion for being classified as related. For these five pairs they tried to infer more precisely the type of relationship from auxiliary information (mtDNA, age, sex, etc.). The results were preliminary and the theoretical basis for the method was mainly outlined.

Pampoulie *et al.* (2013) presented analyses 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. The authors stated that the test-procedure developed during their 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), they were able to find relationships among 15 individuals caught in 2009 and 2010 in Icelandic waters, exhibiting different types of relation, from grandparent to grandchild, to parent and child. 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 conclude about the kind of relationship observed. Considering the relatively low sample size used to perform this analysis, the rate of relatedness among individuals collected within Icelandic waters in two year was considerably high. 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.

DNA sequencing at two allozyme loci

Olsen *et al.* (in press) recently reported the results of an in-depth assessment of the nucleotide sequence at two outlier allozyme loci, malate dehydrogenase (MDH-1) and mannose phosphate isomerase (MPI) in North Atlantic fin whales. Contrary to the allozyme genotyping (Daníelsdóttir *et al.*, 1991b) of the same samples, the DNA sequencing failed to detect any non-synonymous substitutions in either of coding regions at these two allozyme loci. Further analyses of sample quality, predicted protein structure of both the *MDH-1* and *MPI* exon sequences, as well as environmental and morphological variation, which may affect allozyme genotype, suggested that the observed allozyme variation at *MDH-1* and *MPI* is due to alternative splicing and/or post-translational modifications possibly

induced by cellular responses to nutritional stress. The results of Olsen *et al.* (in press) imply that the observed *MDH-1* and *MPI* allozyme variation may not reflect genetic drift, migration, or even selection at the *MDH-1* and *MPI* exons. Consequently the use of those two allozyme genotype data may be inappropriate to infer such population genetic parameter values and should be interpreted with caution. Reported levels of genetic divergence and polymorphisms may not be the product of random genetic drift, migration or even selection. For this reason it is advisable to explore the underlying DNA substitutions and how they correlate with observed allozyme polymorphisms before making any conclusive inference about e.g. population structuring, migration rates, and demographic history from the spatial and temporal distribution of genetic variation at allozyme loci.

SUMMARY OF STOCK DIFFERENCES: WHERE DO WE STAND?

Several types of genetic studies have been performed on the North Atlantic fin whale in the last 20 years, and the main results are difficult to interpret all together. This is partly due to the use of different type of genetic markers, different numbers of genetic markers and different set of samples. The main genetic loci showing high level of divergence among stocks in the North Atlantic were the allozymes, with some loci (*MDH-1* and *MPI*) exhibiting higher levels of differentiation than others (*ADA*, *AK-1* and *SOD-1*). This might, indeed, be interpreted as evidence of selection on allozyme markers, which make them unpractical to assess gene flow among potential stocks. However, a recent sequencing approach (Olsen *et al.*, in press) of the potentially non-neutral loci (under selection, i.e. *MDH-1* and *MPI*) showed that the variation seen at the allozyme level was not detectable at the DNA level, suggesting that levels of genetic divergence and polymorphisms observed at those two allozyme loci may not be the product of random genetic drift, migration or even selection. This results require further investigation before any confirm conclusion can be drawn, but the genetic structure observed in North Atlantic using these markers is questionable until then. The other three markers (*ADA*, *AK-1* and *SOD-1*) showing differentiation have not yet been studied at the DNA level. .

Recent genetic studies performed on other markers known to be neutral (not under the influence of selection) such as mtDNA and microsatellite loci, either revealed very low level of genetic differences among North Atlantic stocks or did not detect any structure at all. Clearly, the genetic approaches performed until now (common genetic approach) have not been appropriate and accurate enough to draw any firm conclusion on stock structure of North Atlantic Fin whale. One alternative approach was proposed by Bérubé *et al.* (2006) who concluded that the most relevant and meaningful measure based on genetic data may be the current migration rates which they estimated using BayesAss. Another potentially more useful approach would be the development of relatedness studies among samples collected at different feeding grounds (IWC stock boundaries considered). The approach presented by Pampoulié *et al.* (2013) proposed the examination of three levels of relatedness, i.e. half-siblings, parent-offspring and first cousins, which are now supported by simulated *P*-values. The examination of the types of relatedness among stocks, and their respective proportion might be an important key to the management of North Atlantic Fin Whale. Indeed, these three categories of relatedness could be used to infer about differential level of family structure among potential stocks which could ultimately be incorporated into management.

FUTURE PERSPECTIVES

The examination of the different genetic studies performed on North Atlantic fin whale is complicated and the results are rather difficult to interpret as it stands nowadays. This is partially due to the complexity of the fin whale biological cycle associated with a recent expansion of its populations (see Pampoulié *et al.*, 2008), but also to the different set-up of the genetic studies. Several alternative methods have been now proposed to ensure proper genetic analyses relevant to the management of the species, such as estimation of number of migrants and relatedness analyses. Ultimately, new genetic markers such as Single Nucleotide Polymorphism (SNPs) might also be more powerful to detect biologically relevant genetic units, especially by combining neutral and selected loci.

However, this review threw the light on one major problem when it comes to genetic analysis of marine mammals, the implication of all concerned institutes into the genetic work performed. This will ensure the combination of all available samples in a single genetic study, which will be easier to interpret than the myriad of manuscripts performed in the last decades using different samples, different number of individuals and different genetic markers. Therefore, we would recommend that further genetic work on fin whale genetic structure be carried out in a large collaborative project involving all the institutes owning samples relevant to the management of the North Atlantic population(s).

Table 1. Summary of genetic studies performed in the North Atlantic. The results are presented by areas-comparisons for the different type of genetic markers. ***N°loci*** indicates the number of loci used; ***n***, the respective numbers of individuals genotyped per regions; ***Level***, the level of differentiation observed either given as: H_{ST} or Φ_{ST} for the mtDNA, F_{ST} values and confidence intervals for the microsatellite loci. ***References*** of the original papers are cited.^a

<i>Areas</i>	<i>Genetic marker</i>	<i>N° loci</i>	<i>n</i>	<i>Level</i>	<i>References</i>
Iceland - Years					
	mtDNA	CR	365	$-0.004 < \Phi_{ST} < 0.01$	Pampoulie <i>et al.</i> , 2008
	Allozymes	11	1134	$0.078 (0.040-0.120)$	Danielsdóttir <i>et al.</i> , 2006a
	Microsatellite	9	903	$F_{ST}=0.005$	Danielsdóttir <i>et al.</i> , 2005, 2006b,c
		15	365	$-0.004 < F_{ST} < 0.026$	Pampoulie <i>et al.</i> , 2008
Iceland vs. Spain					
	<i>Ca</i> locus	1	283/46	$-0.006 < F_{ST} < 0.065$	Danielsdóttir <i>et al.</i> , 2005
	mtDNA	CR	59/39	$-0.001 < H_{ST} < 0.002$	Danielsdóttir <i>et al.</i> , 2006c
		CR	365/43	$-0.004 < \Phi_{ST} < 0.015$	Pampoulie <i>et al.</i> , 2008
	Allozymes	11	283/46	$F_{ST}=0.094 (0.040-0.152)$	Danielsdóttir <i>et al.</i> , 2006a
	Microsatellite	9	903/39	$F_{ST}=0.004$	Danielsdóttir <i>et al.</i> , 2005, 2006b,c
		15	365/43	$-0.008 < F_{ST} < 0.006$	Pampoulie <i>et al.</i> , 2008
Iceland vs. Norway					
	mtDNA	CR	59/40	$H_{ST}=0.003$	Danielsdóttir <i>et al.</i> , 2006c
		CR	365/40	$-0.036 < \Phi_{ST} < 0.026$	Pampoulie <i>et al.</i> , 2008
	Allozymes	11	24/19	$F_{ST}=0.454 (0.000-0.600)$	Danielsdóttir <i>et al.</i> , 2006a
	Microsatellite	9	59/40	$F_{ST}=0.024, 0.002 < F_{ST} < 0.011$	Danielsdóttir <i>et al.</i> , 2006b,c
		15	365/40	$-0.001 < F_{ST} < 0.008$	Pampoulie <i>et al.</i> , 2008
Iceland vs. Canada					
	mtDNA	CR	59/13	$-0.001 < H_{ST} < 0.002$	Danielsdóttir <i>et al.</i> , 2006c
		CR	7-155/13	$-0.054 < \Phi_{ST} < 0.003$	Pampoulie <i>et al.</i> , 2008
	Allozymes	11	24/24	$0.394 (CI: 0.110-0.550)$	Danielsdóttir <i>et al.</i> , 2006a
	Microsatellite	9	59/13	$F_{ST}=0.028$	Danielsdóttir <i>et al.</i> , 2006c
		15	7-155/13	$0.003 < F_{ST} < 0.026$	Pampoulie <i>et al.</i> , 2008
Iceland vs. Greenland					
	mtDNA	CR	59/13	$0.001 < H_{ST} < 0.002$	Danielsdóttir <i>et al.</i> , 2006c
		CR	7-155/13	$-0.054 < \Phi_{ST} < 0.003$	Pampoulie <i>et al.</i> , 2008
	Microsatellite	9	59/13	$F_{ST}=0.000$	Danielsdóttir <i>et al.</i> , 2006c
		15	7-155/15	$0.003 < F_{ST} < 0.026$	Pampoulie <i>et al.</i> , 2008
Norway vs. Greenland					
	mtDNA	CR	59/13	$-0.001 < H_{ST} < 0.003$	Danielsdóttir <i>et al.</i> , 2006c
		CR	40/15	$\Phi_{ST}=0.004$	Pampoulie <i>et al.</i> , 2008
	Microsatellite	9	59/13	$F_{ST}=0.004$	Danielsdóttir <i>et al.</i> , 2006c
		15	40/15	$F_{ST}=-0.006$	Pampoulie <i>et al.</i> , 2008

^a Not that the allozyme and mtDNA results from the 1990's analyses from Danielsdóttir and colleagues were not used to construct this table, as recent re-analyses of the samples were performed in the 2006 manuscripts.

Areas	Genetic marker	N° loci	n	Level	References
Norway vs. Canada	mtDNA	CR	59/13	$H_{ST}=0.005$	Daníelsdóttir <i>et al.</i> , 2006c
		CR	40/13	$\Phi_{ST}=0.108$	Pampoulie <i>et al.</i> , 2008
	Allozymes	11	24/24	$F_{ST}=0.380$	Daníelsdóttir <i>et al.</i> , 2006a
	Microsatellite	9	59/13	$F_{ST}=0.022$	Daníelsdóttir <i>et al.</i> , 2006c
		15	40/13	$F_{ST}=-0.021$	Pampoulie <i>et al.</i> , 2008
Norway vs. Spain	mtDNA	CR	59/39	$0.006 < H_{ST} < 0.010$	Daníelsdóttir <i>et al.</i> , 2006c
		CR	40/43	$\Phi_{ST}=0.025$	Pampoulie <i>et al.</i> , 2008
	Microsatellite	9	59/39	$F_{ST}=0.003$	Daníelsdóttir <i>et al.</i> , 2006c
		15	40/43	$F_{ST}=0.002$	Pampoulie <i>et al.</i> , 2008
Greenland vs. Canada	mtDNA	CR	13/13	$-0.001 < H_{ST} < 0.007$	Daníelsdóttir <i>et al.</i> , 2006c
		CR	15/13	$\Phi_{ST}=0.015$	Pampoulie <i>et al.</i> , 2008
		CR	46/109	$F_{ST}=0.000$	Bérubé <i>et al.</i> , 1998
	Microsatellite	9	13/13	$F_{ST}=0.025$	Daníelsdóttir <i>et al.</i> , 2006c
		15	15/13	$F_{ST}=0.020$	Pampoulie <i>et al.</i> , 2008
		5	46/109	$F_{ST}=0.000$	Bérubé <i>et al.</i> , 1998
Spain vs. Canada	mtDNA	CR	39/13	$0.008 < H_{ST} < 0.013$	Daníelsdóttir <i>et al.</i> , 2006c
		CR	43/13	$\Phi_{ST}=0.058$	Pampoulie <i>et al.</i> , 2008
		CR	39/109	$F_{ST}=0.033$	Bérubé <i>et al.</i> , 1998
	Microsatellite	9	39/13	$F_{ST}=0.019$	Daníelsdóttir <i>et al.</i> , 2006c
		15	43/13	$F_{ST}=0.017$	Pampoulie <i>et al.</i> , 2008
		5	39/109	$F_{ST}=0.001$	Bérubé <i>et al.</i> , 1998
Spain vs. Greenland	mtDNA	CR	39/13	$0.004 < H_{ST} < 0.010$	Daníelsdóttir <i>et al.</i> , 2006c
		CR	43/15	$\Phi_{ST}=0.016$	Pampoulie <i>et al.</i> , 2008
		CR	39/46	$F_{ST}=0.015$	Bérubé <i>et al.</i> , 1998
	Microsatellite	9	39/13	$F_{ST}=0.000$	Daníelsdóttir <i>et al.</i> , 2006c
		15	43/15	$F_{ST}=0.000$	Pampoulie <i>et al.</i> , 2008
		5	39/46	$F_{ST}=0.000$	Bérubé <i>et al.</i> , 1998

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