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Mother-fetus pair analyzes in the Atlantic fin whale *Balaenoptera physalus*: an insight into the migration pattern of the species?

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ABSTRACT

The North Atlantic fin whale *Balaenoptera physalus* undertakes long-distance annual migration between high-latitude summer feeding locations and low-latitude winter mating locations, like most of the baleen whales. However, the uncertainties remaining concerning the mating location and route of migration render any biological investigations challenging. By statistically comparing genotype profiles of mother-fetus pairs (n=21) to that of the potential alleged father (n=139) captured at the same feeding location, we found a matching pairing of a mother-fetus captured in 2009 and a father captured in 2010. To our knowledge, the present study is the first one to detect a mother-fetus pair matching with an alleged father, caught at exactly the same feeding area one year later. This study, based on a very small number of available samples and a small number of loci, therefore reveals that well-planned and organised mark-recapture genetic programs are likely to shed more light into the migration pattern of baleen whale species.

KEYWORDS: BALAENOPTERA PHYSALUS, NORTH ATLANTIC OCEAN, GENETICS, MICROSATELLITE LOCI, MOTHER-FOETUS PAIR, PATERNITY.

INTRODUCTION

In the last decades, several population genetic studies have been carried out on the North Atlantic fin whale stocks (Daníelsdóttir *et al.*, 1992; Daníelsdóttir, 1994; Bérubé *et al.*, 1998; Palsbøll *et al.*, 2004; Daníelsdóttir *et al.*, 2005, 2006; Pampoulie *et al.*, 2008), yet uncertainties remain on the genetic structure of this species.

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

However, other genetic approaches can be developed or employed to investigate potential stock structure in the North Atlantic fin whale. The development of codominant, hypervariable and easily genotyped locus such as microsatellite loci have opened up the possibility for other genetic approaches, which have proven to be a particularly useful alternative when the indirect assessment of gene flow through F_{ST} estimates have failed to reveal any significant signals. It has indeed been recently observed that determining lineage and relation according to genetic markers such as microsatellite loci promises to shed light on the patterns of dispersal of marine organisms (Buston *et al.*, 2007; Hedgecock, 2010; Jones *et al.*, 2010). During the last decade microsatellite loci have therefore proved useful in addressing key empirical questions related to behavioural ecology, biology and mating systems, all of which are relevant in that they are issues that are required in order to understand the dynamic of a species (Bentzen *et al.*, 2001; Fournier *et al.*, 2008; Hedgecock, 2010; Seddon *et al.*, 2005)

Since 2009 Iceland has maintained an individual-based DNA registry for the fin whale, *Balaenoptera physalus* (each individual was screened for 15 microsatellite loci and mtDNA). By statistically comparing genotype profiles of mother-fetus pairs (n=21) to that of the potential alleged father (n=139) captured at the same feeding location, we found a matching pair of a mother-fetus captured in 2009 and a father captured in 2010. Here we report this finding and discuss the results in terms of the migration pattern of the species and population estimates.

MATERIALS AND METHODS

Samples and genotyping

The Icelandic DNA register for the fin whale *Balaenoptera physalus* is composed of 269 genetic profiles collected between the years 2009 and 2010, and has been obtained for 15 microsatellite loci (EV001, EV037, GATA028, GATA053, GATA098, GATA417, GT011, GT023, GT195, GT211, GT271, GT310, GT575, TAA023 and GGAA520; see Appendix 1), the control region of mtDNA and a sex-marker (Bérubé and Palsbøll, 1996). From the 269 individual samples genotyped, a total of 23 females carried a fetus for which a genetic sample was also obtained (4 in 2009 and 19 in 2010). A total of 139 males were collected comprising 67 subjects in 2009 and 72 in 2010. All foetuses were tested against the males collected in

2009 but fetuses from 2010 were only tested against males from 2010 resulting in 1780 paternity tests.

DNA was isolated using Agowa mag Midi DNA Isolation Kit (Agowa GmbH). Polymerase Chain Reactions (PCR) were performed in a 10 μ L volume containing 2 μ L of DNA, 200 μ M of each dNTP, 1X TEG buffer (100 mM Tris-HCl, pH 8.8; 500mM KCl; 15mM MgCl₂; 1% Triton X-100), 0.9 U TEG polymerase (Matis, Taq comparable (Ólafsson *et al.*, 2010)), 0.035-0.125 μ L (100 μ M) of the labeled forward primers and the same amount of reverse primers fitted with a GTTCTT PIG-tail (Brownstein *et al.* 1996). The 15 microsatellite loci, along with the sex-marker, were amplified in four separate multiplex systems (Appendix 1). PCR reactions were performed on a Tetrad2 Peltier (Bio-Rad) thermal cycler as follows: an initial denaturation step of 4 min at 94 °C followed by 30 cycles of 30 s at 94°C, 50 s at variable annealing temperatures (Appendix 1), 50 s at 72 °C, and a final elongation step of 7 min at 72 °C. PCR products were analyzed on an ABI PRISM 3730 sequencer using the GeneScan-500 LIZ size standard, and genotyped with GeneMapper 4.0 (Applied Biosystems). Many of the primers used in this study were redesigned at Matis, where the published loci from GenBank and authors were used as templates (Appendix 1). As the genotyping with the published primers for loci TAA023 (Palsbøll *et al.*, 1997) and GT271 (Bérubé *et al.*, 2000) was relatively unsuccessful, new primers were developed for these loci after the sequencing of a few fin whale samples upstream and downstream of the original loci using the gene retrieval method (Turner *et al.* 2005). Both TAA023 and GT271 were originally isolated from the humpback whale (*Megaptera novaeangliae*). The sequencing results of the fin whale samples showed divergences between the original humpback whale forward primer sequence and the reverse primer site for TAA023 and GT271, respectively. Therefore, a new forward primer was designed for the TAA023 locus and new reverse primer for the GT271 locus. The reverse primer site was conserved between the two species for TAA023, although a new and improved primer was designed for the reverse primer as well. The forward primer site for GT271 was conserved, and since the pre-published reverse primer worked well for the fin whale it was consequently used again in this study (Bérubé *et al.*, 2000).

Statistical analyzes

The software WHICHPARENTS (available at <http://www-bml.ucdavis.edu/whichparents.html>) was used to assess potential crosses among mother-fetus and alleged father, using 0-4 potential misses. WHICH PARENTS is an exclusion based program which presents a moderate level of correction for null alleles, genotyping errors and mutation (handled by misses).

Additional analyses of the possible crosses were performed in the software PATCAN v1.2 (available on request to J.A. Riancho; Riancho and Zarrabeitia, 2003) to assess the paternity probability of the alleged father. The standard results reveal the likelihoods and probability of the alleged father being the true father, versus the alternative hypothesis of the true father being an unrelated individual. The software also allows for inclusion of mutation rate at exclusive loci.

Paternity tests were also performed using CERVUS 3.0.3 (Kalinowski *et al.*, 2007) for the 23 fetus collected and the 139 candidate fathers genotyped. In the simulation of paternity analyzes, the proportion of loci typed was 0.95 for the full set of loci and the simulated genotyping error rate was set at 0.01. Critical values of Delta were assessed for 80 and 95% confidence level based on simulation of 100,000 offsprings.

RESULTS

The exclusion program WHICHPARENTS revealed the presence of one possible cross between a mother-foetus pair and an alleged father when run with a 0 miss procedure, i.e. a 100% match (Table 1).

Table 1. Allele sizes at each microsatellite loci of the mother-foetus pair number F09-091 and of the alleged father (F10-100). The alleged father was collected in 2010 while the mother-foetus pair was collected in 2009.

Locus	Mother	Foetus	Alleged father
EV1	157/163	159/163	159/171
EV37	193/193	193/193	193/193
GT011	127/131	125/131	117/125
GT023	127/129	125/129	125/129
GT195	161/175	161/169	169/173
GT211	120/120	116/120	116/116
GT271	114/118	114/118	118/118
GT310	106/112	106/112	112/112
GT575	154/156	154/154	152/154
GATA028	199/219	199/215	215/227
GATA053	262/262	262/270	258/270
GATA098	100/100	096/100	096/108
GATA417	269/277	269/269	269/285
GGAA520	201/223	207/223	207/219
TAA023	086/086	086/086	086/086

The analysis of this possible family, involving the mother F09-091, her foetus (F09-091F) and the alleged father (F10-100), using the software PATCAN revealed a high likelihood and probability (cumulative $P_w = 1$; cumulative $PI > 2.7 \times 10^{12}$) associated with the hypothesis that the alleged father was the true biological father of the foetus F09-091F (Table 2).

Table 2. Bayesian analysis of the mother-foetus pair F09-091 and the alleged father F10-100 by the software PATCAN (Riancho and Zarrabeitia, 2003). The values represent the likelihood and the probability associated with the hypothesis that the alleged father is the true biological father versus the competing hypothesis that the father is an unrelated animal. PI depicts the paternity index.

Prior probability (%)	Prior odds	PI	Posterior odds	Posterior probability
0.1	0.001001	$>10^6$	2.6×10^8	100
1	0.010101	$>10^6$	2.6×10^9	100
10	0.111111	$>10^6$	2.6×10^{11}	100
50	1	$>10^6$	2.6×10^{12}	100
70	2.333333	$>10^6$	6.2×10^{12}	100
90	9	$>10^6$	2.4×10^{13}	100
95	19	$>10^6$	5.1×10^{13}	100

The paternity analysis performed with the program CERVUS predicted a very low success rate of paternity assignment (Table 3) but slightly higher than the simulated data (not shown), at least for the father alone set-up.

Table 3. Number of paternity assignment among the 23 fetus with known mother calculated in CERVUS.

Confidence level of assignment	Father alone			Father given known mother		
	Critical delta	Observed assignment	Expected assignment	Critical delta	Observed assignment	Expected assignment
95%	3.92	1 (5%)	3 (15%)	0	2 (9%)	3 (16%)
80%	0.93	4 (18%)	4 (19%)	0	2 (9%)	3 (16%)
Unassigned		18 (82%)	18 (81%)		20 (91%)	19 (84%)
Total		22 (100%)	22 (100%)		22 (100%)	22 (100%)

When a mother-fetus pair is genotyped, one can consider that one male (father) has been marked (with replacement as one male may father many). A capture occurs when a male is caught and genotyped. A recapture occurs when an alleged father matches a mother-foetus pair. The number of observations (the available markings times the captures) from males caught in 2009 (ignoring male mortalities from the time of impregnation to capture in the following season) is 268 (4*67) in 2009 and in 2010 assuming annual natural survival of 0.96 for mature males is 1,645 (19*72+4*72*0.96) or in total 1,913. With one recapture the most likely estimate of the number of potential fathers to females in the area is therefore 1,913 and for a 90% probability of more recoveries, or fewer, the numbers are 510 and 18,820. An unbiased estimate is around 908.

DISCUSSION

The fin whale *Balaenoptera physalus* is believed to undertake long-distance migration between high-latitude feeding areas in the summer and low-latitude mating locations in the winter, like most of the baleen whales; in spite of this, very little is known about the actual migration pattern and dynamic of this species. Although several genetic studies have been performed over the last few decades, no consensus could be reached upon the potential numbers of mating locations and on the migration pattern of the species.

In an attempt to assess the migration route of this species, acoustic (Castellote *et al.*, 2010) and ID photography (Coakes *et al.*, 2005) have been implemented, as well as different tagging techniques (Ray *et al.*, 1978; Watkins *et al.*, 1996). However, none of these methods provided conclusive evidence for a migration route/pattern for the targeted species, although acoustic data did reveal that fin whale from East and West Iceland might occasionally enter the southwest Mediterranean basin during their wintering migration (Castellote *et al.*, 2010). Nieukirk *et al.* (2009) detected year round fin whale calls on either side of the Mid-Atlantic Ridge from 16 to 51°N, with a peak in winter and a shift farther north in summer.

Here, despite the low number of available samples, searching within the Icelandic DNA registry for a potential match between a mother-fetus pair and an alleged father enabled us to find a highly significant match between a mother-fetus pair caught in 2009 and an alleged father caught in 2010.

This match might be incidental and can be discussed due to the low number of loci employed, and at least hypotheses can still be considered to explain the observed trio-match:

1- The detected mating pair occurring at the same mating location exhibited a similar migration habit during the winter. Sighting surveys revealed that fin whales are most commonly seen alone or in “pairs” (Vikingsson *et al.*, 2009) and relatedness analyses tended to confirm that related individuals (Parent-offspring and half-sibling) more commonly occur at the same feeding location (Skaug *et al.*, 2008). Therefore, although more information will be required to confirm this hypothesis, it is plausible to suggest that related individuals, originating from the same mating location, exhibit an identical migration route and sense of timing.

2- The detected mating pair may originally belong to two different populations (or mating locations) among which gene flow may not be restricted, which might indicate that individual fin whale from different mating location may roam across the North Atlantic during the winter feeding migration as was suggested by a previous genetic study (Pampoulie *et al.*, 2008).

In addition, this matching trio enables us to give another estimate of population size similar to what has been previously calculated. Indeed, population estimates from sightings surveys for the West Iceland area (incorporating the whaling grounds) as defined by the IWC for RMP-IST have been in the range 5 to 10,000 animals and for the wider EGI IWC-Schedule area of 20-30,000 animals. The other observations of relevance here are given in Gunnlaugsson *et al.* (2010) and include discovery mark recoveries and parent offspring detections from genotypes. Discovery mark recovery estimates based on first and second year recoveries within the area are around 3,000 (n=23), but increase with time, while estimates based on markings outside are high, but decrease with time. A parent-offspring estimate from within the area was in the range of 5 to 10,000. Although the confidence limits are wide we have here presented yet another observation of incomplete mixing, in the short term, of animals on the ground west of Iceland to the wider population.

To conclude, this study does not seek to resolve the issue on the potential number of mating locations of the fin whale based on this unique matching trio but it nevertheless suggests that an intensive and well-organised genetic mark-recapture program could shed more light into the migration pattern of *Balaenoptera physalus* and other baleen whales than genetic structure studies, so long as the mating location(s) is (are) not known.

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Fin whale paternity analyzes

Appendix 1 Characteristics of the 15 microsatellite DNA markers scored for 269 fin whale individuals collected for the Icelandic DNA registry.

Locus	Original primer sequence (5'→3')* Forward and reverse primers	Reference	Redesigned primer sequence (5'→3')* Forward and reverse primers	Multiplexes	Ann. T°C	Size range	No. of alleles
EV01	CCCTGCTCCCCATTCTC ATAAACTCTAATACACTTCCTCCAAC	Valsecchi and Amos (1996)		1	54°C	143-177	15
EV037	AGCTTGATTGGAAGTCATGA TAGTZGAGCCGTGATAAAGTGC	Valsecchi and Amos (1996)	AGCTTGATTGGAAGTCATGAA GTGCAACCATAATGGAAAAACC	1	54°C	179-215	17
GATA028	AAAGACTGAGATCTATAGTTA CGCTGATAGATTAGTCTAGG	Palsboll <i>et al.</i> (1997)		2	56°C	191-239	13
GATA053	ATTGGCAGTGGCAGGAGACCC GACACAGAGATGTAGAAGGAG	Palsbøll <i>et al.</i> (1997)	ATTGGCAGTGGCAGGAG	3	58°C	246-278	9
GATA098	TGTACCCTGGATGGATAGATT TCACCTTATTTTGTCTGTCTG	Palsbøll <i>et al.</i> (1997)	TGTACCCTGGATGGATAGATTG	1	54°C	92-120	8
GATA417	CTGAGATAGCAGTTACATGGG TCTGCTCAGGAAATTTTCAAG	Palsbøll <i>et al.</i> (1997)	TAATGGAAATGTTCTCTATCCTG	2	56°C	209-297	19
GT011	CATTTTGGGTTGGATCATTC GTGGAGACCAGGGATATTGC	Bérubé <i>et al.</i> (1998)		3	58°C	117-133	8
GT023	CATTTCTACCCACCTGTCAT GTTCCCAAGGCTCTGCACTCTG	Bérubé <i>et al.</i> (2000)	GTTCCCAAGGCTCTGCACTC CATTTCTACCCACCTGTC	1	54°C	97-143	12
GT195	TGAGAAAAGATGACTATGACTC TGAAGTAACAGTTAATATACC	Bérubé <i>et al.</i> (2000)	GGTGAGAAAAGATGACTATGAC GATTTGAAGTAACAGTTAATATACC	3	58°C	161-181	10
GT211	CATCTGTGCTTCCACAAGCCC GGCACAAGTCAGTAAGGTAGG	Bérubé <i>et al.</i> (2000)	CTGCTCTATTCTATGAAAGCATTG CTCCAGTATACCTATCTTGTC	2	56°C	106-126	11
GT271	GCTCACACTGGTAATCTGTGG CCCTAGGAAGGATAGACATAG	Bérubé <i>et al.</i> (2000)	ATAGAGCTAGGAAAGATAGAC	4	58°C	108-128	10
GT310	TAACTTGTGGAAGATGCCAAC GAATACTCCCAGTAGTTTCTC	Bérubé <i>et al.</i> (2000)	GAATACTCCCAGTAGTTTCTC TAACTTGTGGAAGATGCCAAC	1	54°C	106-130	11
GT575	TATAAGTGAATACAAAGACCC ACCATCAACTGGAAGTCTTTC	Bérubé <i>et al.</i> (2000)	CCAATATAAGTGAATACAAAGACCC	2	56°C	146-168	9
TAA023	CTCGCACAGAAATGAAGACCC AGAGCCTGAACCAGAACAAGG	Palsbøll <i>et al.</i> (1997)	CTAGCCGCAACCGGAGAAAAG CCTGAACCAGAACAAGGTAAC	4	58°C	86-104	7
GGAA520	TAGCAGAYCTGAGTTATTTCC TAGCATTTTAGTCTTGGGTGG	Palsbøll <i>et al.</i> (1997)	TAGCAGAYCTGAGTTAATTCC	4	58°C	199-235	15