Population structure of bycaught harbour porpoise (*Phocoena phocoena*) in Norway

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No potential conflict of interest was reported by the authors

Availability of data

The authors confirm that the data supporting the findings of this study are available within the article [and/or] its supplementary materials (i.e. Supplementary File_Raw data).

ABSTRACT

The preference for coastal habitats makes the harbour porpoise, *Phocoena phocoena*, vulnerable to fisheries conflicts and hence prone to die due to entangling in fishing nets. An opportunistic sampling of such casualties (134 individuals) in Norwegian waters was used to assess the genetic population structure of the species by SNP-genotyping at 78 loci. The results of genetic clustering obtained for these individuals failed to identify more than one genetic group. Likewise, the individually based F_{ST} did not meet an Isolation-by-Distance pattern, thus supporting the conclusion that harbour porpoise in Norway probably belong to a single genetic group or population.

INTRODUCTION

Unravelling the factors that influence genetic variation and population structure is fundamental in ecological genetics (Storfer *et al.* 2010). Patterns of genetic differentiation often reflect spatial variation in gene flow, and landscapes can influence gene flow through geographic and environmental variation and their combined effects. In the marine environment, dispersal of mobile species such as cetaceans is rather unconstrained across vast distances, albeit they may display genetic and morphological differentiation over small geographic scales for reasons such as behavioural traits, prey availability/choice, social structure, habitat use or oceanographic processes (see Hoelzel 2009, Vachon *et al.* 2018 for a review). Resolving the underlying causal mechanisms behind the emergent genetic patterns is important for the management and the conservation of the genetic diversity of the species.

The harbour porpoise (*Phocoena phocoena*) is one of the smallest and most abundant cetaceans, inhabiting most shelf and coastal waters in the Northern Hemisphere (e.g Palumbi 1994, Fontaine 2016). Three allopatric subspecies have been recognized in agreement with morphological and genetic differentiation (Rice 1998): *P. p. vomerine* (Gill, 1865) in the North Pacific, *P. p. phocoena* (Linnaeus, 1758) in the North Atlantic (e.g. Palumbi 1994, Hoelzel 1998, Fontaine *et al.* 2007) and *P. p. relicta* (Abel, 1905) in the Black Sea (Rosel *et al.* 1995, Tolley & Rosel 2006, Viaud-Martínez *et al.* 2007, Fontaine *et al.* 2012). Recently, a fourth subspecies, *P. p. meridionalis*, has been suggested in

the southern waters of the Northeast Atlantic off the Iberian Peninsula and Mauritania (Fontaine *et al.* 2014, Fontaine 2016).

The use of coastal habitat together with their piscivore feeding behaviour makes this species particularly vulnerable to incidental catches in gillnets (e.g. Read *et al.* 2006, Bjørge *et al.* 2013). The recommendations by ASCOBANS (Agreement on the Conservation of Small Cetaceans of the Baltic, North East Atlantic, Irish and North Seas) state that annual bycatches should not surpass 1.7% of the best population estimate (ASCOBANS 2000), whereas the most recent estimate in Norwegian coastal waters was of ca. 3000 bycaught individuals (Bjørge & Moan 2017). Whether these numbers are sustainable is highly dependent upon the abundance and populations structure of the species in this area. Unfortunately, there is no abundance estimate for the whole Norwegian coast, however, the abundance of harbour porpoise from 62°N to 68°N was estimated to be 24526 individuals (CI_{95}: 14035-40829) in 2016 (Hammond *et al.* 2017).

The body of literature addressing the population genetic structure of harbour porpoises has been growing during the last two decades, and deals separately with different areas of their distribution range (reviewed in Fontaine 2016). In Norwegian coastal waters, two studies based on few microsatellite DNA markers suggest lack of genetic structure (Andersen *et al.* 2001, Fontaine et al. 2007). However, an amphi-Atlantic integrative study enabling to put the stock specific levels of diversity and divergence into perspective is still lacking, and therefore hampering optimal management advice and practices.

The aim of the current study is, therefore, to assess the genetic structure of harbour porpoise along the Norwegian waters by SNP-genotyping of 134 bycaught animals collected in 2016 and 2017.

METHODS

A total of 134 individuals (58 females and 76 males), incidentally bycaught in gillnets, were collected in September-October 2016 and February-April 2017 in Norwegian coastal waters (Fig. 1). A total of 21 females (36.2%) carried foetus, which were genotyped although not included in the study. Tissue samples, stored in 95% EtOH, were used to isolate DNA in 96-well plates, using the Qiagen DNeasyH96 Blood & Tissue Kit.

The suite of SNPs for genotyping was identified from ddRAD-sequencing data made available in the GenBank by Lah *et al.* (2016). Sequences corresponding to nine of the individuals in the aforementioned study were aligned against the beluga genome (https://www.ncbi.nlm.nih.gov/assembly/GCF_002288925.1/) to identify SNPs using the Burrows-Wheeler Aligner, BWA (Li & Durbin 2009). Polymorphic sites were detected using the *mpileup* function from the package SAMtools (Li *et al.* 2009, Li 2011). SNPs were filtered for having at least 10x coverage in at least 7 samples out of nine. To choose markers distributed across the genome, 151 SNP were retained, each one on a different genome contig. The selected SNPs were located on contigs of size varying from 96Mb to 12Kb. Primers were designed, and 114 of the 151 retained assays were fitted into four multiplex reactions. After purging markers due to poor clustering or bad amplification, the suite of SNPs was reduced to 78 loci (see Table S1 in Supplementary Information, for details). SNP locus primer design, amplification and genotype calling was based on the Sequenom MassARRAY iPLEX Platform, as described by Gabriel *et al.* (2009).

Foetuses were discarded from the statistical analyses; however, they were used to investigate if any of the males present in the samples could have fathered them. Paternity tests were conducted with VITASSIGN V8-5.1.xlsm (Vandeputte *et al.* 2006), an exclusion method that relies on the incompatibilities between parents and putative offspring regarding Mendelian inheritance rules, and therefore very sensitive to genotyping errors or mutations. To overcome this drawback, the program was tested by allowing for one mismatch (one incompatible allele allowed) and two in a scheme allowing for all possible couple combinations.

Genetic diversity was assessed through observed (H_o) and unbiased expected heterozygosity (uH_e) as well as the inbreeding coefficient (F_{IS}), all of which were computed with GenAlEx (Peakall & Smouse 2006). Possible linkage between all locus pairs (Linkage Disequilibrium, LD) was investigated using the program GENEPOP 7 (Rousset 2008). Likewise, the genotype distribution of each locus and its direction (heterozygote deficit or excess) in comparison with the expected Hardy-Weinberg distribution (HWE) was also addressed with the same program. Both were examined using the following Markov chain parameters using 10000 steps of dememorization, 1000 batches and 10000 iterations per batch, and signification was assessed after the sequential Bonferroni correction (Holm 1979).

Two approaches were used to investigate genetic structure and therefore to determine the number of genetic groups in which our samples could be divided. First, the Bayesian-based clustering algorithm implemented in STRUCTURE (Pritchard *et al.* 2000), where genetic groups were identified after ten runs with a burn-in period consisting of 100000 replications and a run length of 1000000 MCMC under a model assuming admixture and correlated allele frequencies within a range of clusters (K) from 1 to 5. STRUCTURE output was analysed using the *ad hoc* summary statistic ΔK of Evanno et al. (2005), together with the four statistics (MedMed, MedMean, MaxMed and MaxMean) implemented in StructureSelector (Li & Liu 2018). Finally, the ten runs for the selected K were averaged with CLUMPP v.1.1.1 (Jakobsson & Rosenberg 2007) using the FullSearch algorithm and the G' pairwise matrix similarity statistic, and were graphically displayed using barplots. Second, the inference on clusters of genetically related individuals was conducted using the *Find.clusters* function within the Discriminant Analysis of Principal Components (DAPC) implemented in *adegenet* (Jombart 2008).

Isolation-by-Distance (IBD) is the standard approach to express the genetic differentiation as a function of the geographic distance. Given that the spatial distribution of the harbour porpoise samples did not allow to distribute them into discrete groups, the pattern of IBD was investigated using an individual approach. Thus, a matrix of individual-level pairwise F_{ST}, which generalize the F_{ST} between two populations to pairs of individuals, was computed with the R-package "popkin" ("population kinship") (Ochoa & Storey 2018). When individuals are locally outbred and locally unrelated, the pairwise F_{ST} is given in terms of the inbreeding and kinship coefficients (see Ochoa and Storey (2016). The matrix of geographic distances was obtained from the spatial coordinates of individual bycatches using the Geographic Distance Matrix Generator v1.2.3 (Ersts 2006). IBD was assessed with PASSaGE 2 (Rosenberg & Anderson 2011) via a two-tailed Mantel test, and significance was tested after 10000 permutations.

The statistical power of our set of 78 SNP loci to detect genetic differentiation was assessed using the POWSIM software ver. 4.1 (Ryman & Palm 2006). This software estimates whether the observed data set carry the sufficient statistical power, i.e. ≥80% according to Ryman and Palm (2006), to detect a F_{ST} significantly larger than zero using Chi-square and Fisher tests. The percentage of

significant outcomes (at α= 0.05) for a range of predefined F_{ST}-values (0.001-0.02) obtained for 1-20 generations of drift (t) was interpreted as the power to detect the defined level of genetic divergence. Allele frequencies were estimated with GenAlEx, and 1000 iterations per run were conducted using 1000 dememorizations, 100 batches and 1000 iterations per batch (default settings) while keeping effective population size (Ne) constant at 500.

RESULTS

The raw data are available in Supplementary Information. None of the males sampled were identified as the father of any of the 21 foetuses, even when allowing for two mismatches, *i.e.* incompatible alleles for each sire-dam-offspring triplet.

After Bonferroni correction, eight out of the 78 loci showed significant heterozygote deficiencies whereas no departures from linkage disequilibrium were observed. The distribution of the samples was slightly biased towards the north in 2017 compared with 2016 although no genetic differentiation was recorded between sampling years (F_{ST}=0.001, P=0.2112), nor between sexes (F_{ST}=0.002, P=0.075).

STRUCTURE showed the highest average likelihood at K=1 (LnP(K)= -11390.97). The probability at K=2 was some 8% lower (LnP(K)= -12378.33) and this decreasing trend continued across consecutive values of K. Likewise, three out of the four estimators of StructureSelector pointed at K=1 as the most likely number of clusters. The fourth estimator pointed at K=2 in agreement with Evanno test, which by definition always shows K>1, and selected K=2 with low support (ΔK=7.3). The individual inferred ancestry hardly reached 60%, thus making impossible to reliably assign individuals to any of the two putative clusters. Finally, the Bayesian information criterion (BIC) implemented in the *Find.clusters* function reported almost identical values for K1 and K2. Hence, both approaches rendered K=1 as the most likely scenario.

The simulation-based calculation of the statistical power conducted with POWSIM revealed that the SNPs dataset used for genotyping has the capacity to detect significant differentiation for F_{ST} >0.0095 (Fig. 3). Given that the F_{ST} between sampling years or sexes was ≥0.0095, the lack of resolution of the dataset does not seem to account for the observed lack genetic differentiation.

The individual-based F_{ST} matrix calculated with *popkin* for the full set of individuals did not follow an Isolation-by-Distance pattern (Mantel's r=0.0183, P=0.323).

DISCUSSION

The 134 harbour porpoises analysed in this study appear not to be genetically structured and therefore most likely belong to the same genetic group. These findings consistently align with previous studies using microsatellite markers (Andersen et al. 2001). Also using ten microsatellites, Fontaine et al. (2007) divided the North Atlantic harbour porpoises into three genetic clusters; two of them, which extended from the North Sea (≈53 °N) to the northernmost of Norway (≈71 °N), showed an extremely low, albeit statistically significant differentiation (F_{ST}<0.001). The statistical significance achieved by this small differentiation could be explained by the number of individuals analysed, which was 4.8 fold larger than ours (also in a broader geographic scope). Hence, this virtually null genetic differentiation is in agreement with the picture of one single cluster that both STRUCTURE and *Find.clusters* suggested for our data.

Our suite of 78 biallelic SNPs revealed statistical power to correctly detect values of F_{ST}>0.0095; in agreement with the F_{ST} > 0.008 that Chehida *et al.* (2019) reported for a suite of ten microsatellites (and 84 different alleles) genotyped on 144 harbour porpoises from the Black Sea and adjacent waters. Likewise, using a theoretical approach, in cases of low F_{ST} (0.0025), power only reached 80% when 75 SNPs and 100 samples per population were used (Morin *et al.* 2009).

Harbour porpoises in the Norwegian waters belong to the eastern North Atlantic group, which behaves as a 'continuous' population displaying a significant pattern of isolation-by-distance (Fontaine et al. 2007, Lah et al. 2016). The IBD pattern, which gets revealed when the amplitude of the geographic range explored exceeds thousands of kilometres and goes unnoticed when zooming on a smaller section, was not observed in our data due to the lack of correlation between geographic distance and the individually-based F_{ST} matrix for the 134 genotyped individuals.

The mismatch between management regimes and genetic or biological evidence represents a major challenge to the sustainable exploitation of marine resources (Reiss *et al.* 2009). A precautionary approach consisting in dividing the harvest areas into small units to potentially account for underlying

or cryptic population genetic structure in absence of alternative evidence is sometimes used for direct management, or as for harbour porpoises, indirect exploitation through bycatch. This would be the case of the minke whale (*Balaenoptera acutorostrata*) in the Northeast Atlantic, where the combined Norwegian commercial harvest based upon the International Whaling Commission (IWC) advice is divided between multiple management areas each with their own separate quota, despite the fact that the analysis of some 3000 whales in the period 2004-2011 clearly showed that the species is probably represented by a single panmictic population in this area (Glover *et al.* 2012, Quintela *et al.* 2014). Likewise, the IWC demands the harbour porpoises in Norway to be managed as two independent stocks: i. NOR, which comprises North-west/Central-west Norway together with the Barents Sea and ii. NENS, which includes North-eastern North Sea and Skagerrak (Evans *et al.* 2009). This arbitrary boundary, coincident with the parallel 62°, corresponds to the management division that has been given for other marine species such as coastal cod (*Gadus morhua)* and plaice (*Pleuronectes platessa*). However, in the current dataset, the number of individuals sampled south to parallel 62° did not allow for any robust assessment of genetic differentiation, and therefore the accuracy of such a division cannot be reliably tested and awaits for further evaluation. Furthermore, under a new proposal (NAMMCO & IMR 2019), the NENS-stock should account separately for Kattegat and Belt Seas. This subdivision is in agreement with the genetic differentiation found between harbour porpoises sampled in Danish and Norwegian waters (De Luna *et al.* 2012); differentiation that is accompanied by phenotypic divergence in terms of the buccal cavity.

Finally, to fully elucidate the population structure of harbour porpoise, a comprehensive study covering both sides of the Atlantic with a large number of both genotyped individuals and molecular markers seems essential.

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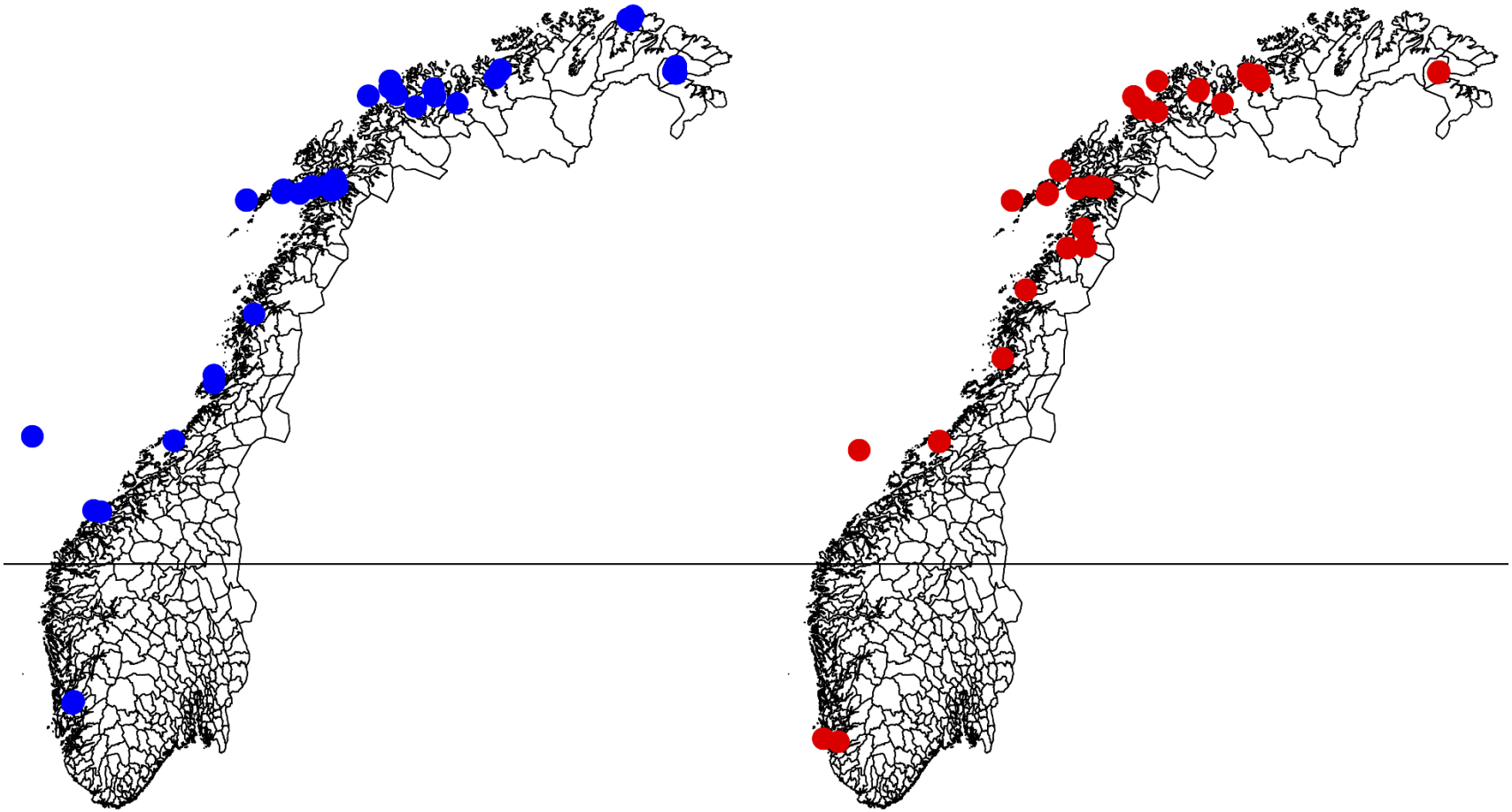

Fig. 1.- Position of the individual harbour porpoises bycaught in gillnets in Norwegian waters. Blue dots depict males whereas red dots depict females and the line represents the parallel 62 °N, which delimits IWC management areas within the Norwegian coast.

330

331 **Fig. 2.**- Bayesian clustering of the 134 adult harbour porpoises genotyped at 78 SNP loci. The barplot represents the estimated membership after averaging

332 ten STRUCTURE runs at K=2 with CLUMPP. The order of the individuals in the plot, starting from the left, depicts decreasing latitude of sampling locations.

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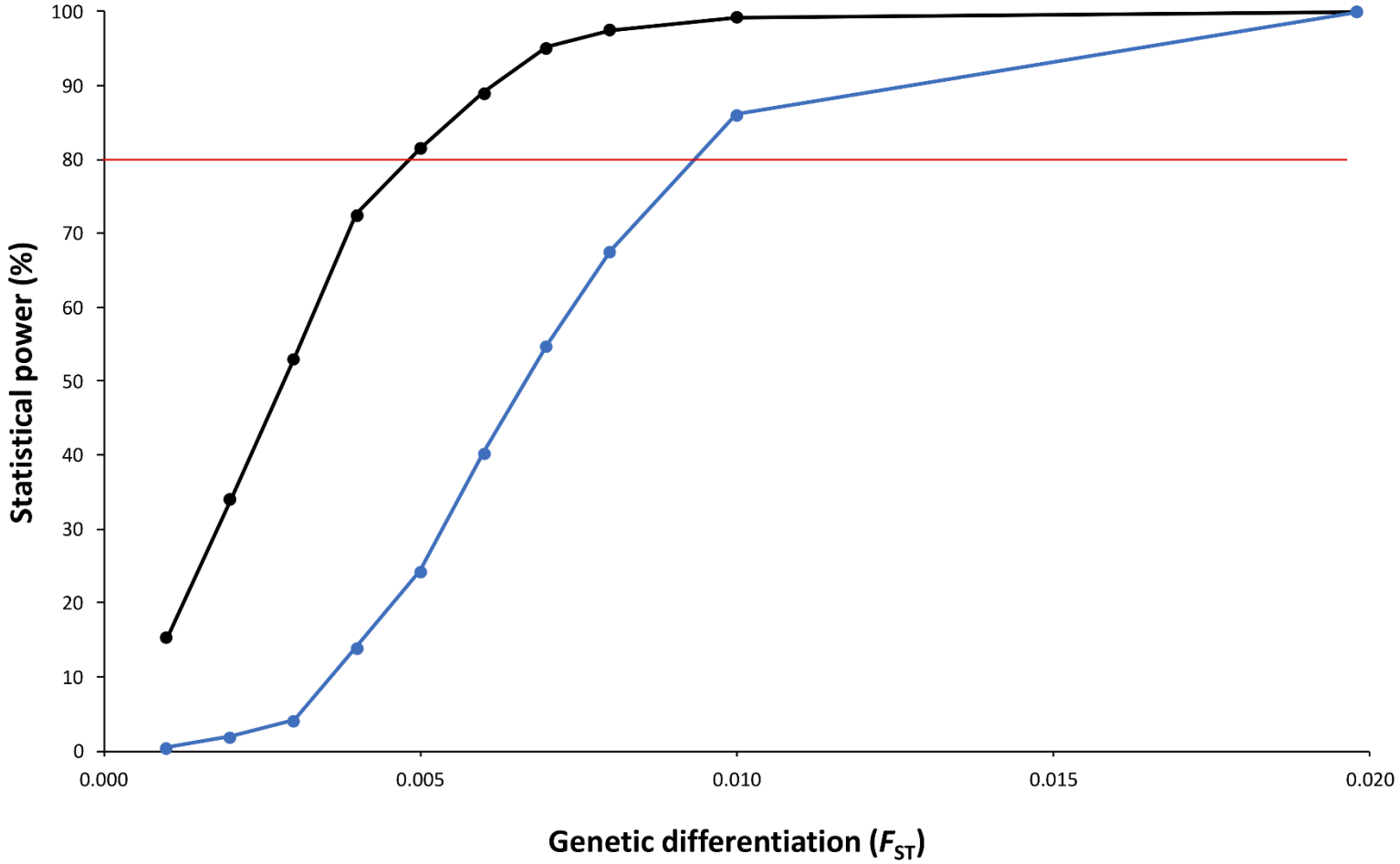

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335 **Fig. 3.**- Statistical assessment of power to detect significant differentiation between two populations conducted with POWSIM. The red line depicts the
336 power threshold of 80% following the recommendations by Ryman and Palm (2006). The suite of 78 SNP loci showed the capacity to detect significant
337 differentiation from F_{ST}=0.0095.