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Phylogenetic analysis of killer whale (*Orcinus orca*) and humpback whale (*Megaptera novaeangliae*) populations along the Northern Norwegian fjords and adjacent waters

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Foreword

The purpose of this study was to investigate the identity of the killer whales and humpback whales gathering in Northern Norway to feast on the Norwegian Spring Spawning (NSS) herring, and to shed light on the phylogenetic position these individuals hold in the global context of each species. This project is a part of the Whalefeast Project, an initiative funded by the Norwegian Research Council to improve the understanding of the relation of these cetaceans with the NSS herring and their presence in Northern Norway.

The samples used in this study were gracefully provided by Audun Rikardsen.

This Master's thesis is written in an article format.

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To Kim Præbel, my main supervisor, thank you for checking up on me, pushing me forward, and bringing out the best biologist in me, always. It has not been my easiest achievement, writing a master's thesis under a worldwide pandemic, and just a stone's throw away from the North Pole. In a weird set of circumstances that put me in quarantine, Kim was so kind as to offer to do my groceries, and I sent him a shopping list. From the supermarket, he calls and has one question: "Why is there no chocolate on your list?". Well, what can I say, that's my kind of supervisor. Tak, Kim!

1 Abstract

Killer whales (*Orcinus orca*) and humpback whales (*Megaptera novaeangliae*) are two widely distributed cetacean species and both seasonally congregate in the waters off the fjords in Northern Norway to feast on the Norwegian Spring Spawning herring (*Clupea harengus)*. With phylogenetic analysis of complete mitochondrial genomes, obtained by shotgun sequencing, from individuals sampled through four years, this study has attempted to shed light on the geographical origin and phylogenetic position of Norwegian killer whales and humpback whales in the global context of each species. In total, 19 haplotypes were identified among 134 killer whales, and 18 haplotypes were identified among 94 humpback whales. The killer whales sampled in Northern Norway showed structuring between individuals and cluster in a clade with other individuals from Eastern North Atlantic Ocean previously described in literature. The humpback whales showed less clear clustering within the global context but have revealed a potential connection of four individuals with haplotypes from the Southern Hemisphere. Overall, this study suggests that the feeding aggregations in Northern Norway gather killer whales mainly from Eastern North Atlantic Ocean, and humpback whales from the North Atlantic and possibly from the South Atlantic Ocean.

2 Introduction

Killer whales (*Orcinus orca* Linnaeus, 1758) are widely distributed through all of the world's oceans (Matkin & Leatherwood, 1986), and feed on a variety of prey types (Bloch & Lockyer, 1988, Foote *et al*. 2009, Deecke *et al*. 2011, Ryan & Holmes, 2012, Foote *et al*. 2013), including over 140 species (Cosentino, 2015). These whales are widely acknowledged as an exceptionally successful species, which seems to be linked to their unique ability to adapt behaviour depending on the available prey, and to change their hunting strategies accordingly (Bruyn *et al*. 2012). The energetic cost of teaching and learning such specified foraging techniques seems to render it advantageous to focus mainly on one prey type, possibly leading to the clan-specific behaviours that characterize the species (Yurk *et al*. 2002). Although it has been suggested that they be divided into multiple species (Morin *et al.* 2010), killer whales are still considered a single species, with currently ten ecotypes acknowledged by NOAA (2016). Five occur in the

Southern Hemisphere, namely Antarctic killer whale (type A), Pack ice killer whale (large type B), Gerlach killer whale (small type B), Ross Sea killer whale (type C) and Subantarctic killer whale (type D). The remaining five occur in the Northern Hemisphere: Resident killer whale, Transient (Bigg's) killer whale and Offshore killer whale (all from the Eastern North Pacific), Type 1 Eastern North Atlantic (ENA type 1) and Type 2 Eastern North Atlantic (ENA type 2).

Foote *et al.* (2009) proposed the two types of North Atlantic killer whales, (ENA type 1 and ENA type 2) based on tooth wear pattern, nitrogen stable isotope ratios and mitochondrial DNA (mtDNA) sequences. The two groupings correlate with diet and size, suggesting, respectively, a generalist Type 1 with males reaching up to 6,6m in length, and a specialist Type 2, in which males reach up to 8,5m (Foote *et al.* 2009). In a later study, through analysis of the mtDNA control region and microsatellite genotyping, Foote *et al.* (2011) identified three North Atlantic killer whale populations: one associated with mackerel, a second one partly associated with bluefin tuna, and a third one associated with North Atlantic herring, including NSS herring. These would all fall under the generalist Type 1, since is it has been suggested that Type 2 feeds mainly on other cetaceans (Foote *et al.* 2009). Blubber fatty acid signature analysis has also proposed that the diet of North Atlantic killer whales varies according to region and/or season (Bourque *et al.* 2018)

Humpback whales (*Megaptera novaeangliae* Borowski, 1781) are likewise widely distributed (Jackson *et al.* 2014). They are divided into three oceanic populations, with suggested subpopulations within each, but evidence of migration between ocean basins is very limited (Baker *et al.* 1993). They are known to undertake the most extensive migrations between feeding and breeding grounds of all mammals (Jackson *et al.* 2014). Individual whales have, for example, been observed in the Norwegian Sea and then identified in low latitude feeding grounds in Trinidad, in the South Eastern Caribbean, both with haplotype analysis of the mtDNA control region (Bérubé *et al.* 2004) and through photographic records (Stevick *et al.* 1998). This is consistent with known migration routes between the North Atlantic breeding grounds, in Northern Norway and the Barents Sea, Iceland, Newfoundland and the Gulf of Maine, and the North Atlantic feeding grounds, in the Caribbean and possibly around Cape Verde (Ruegg *et al.* 2013). Humpback whales are considered generalists in their diet, which consists mainly of zooplankton and pelagic schooling fish, but the proportion of different components has been shown to change between years (Witteveen *et al.* 2012).

Based on a two-decade study, North Atlantic killer whales have been documented to show high site fidelity to spawning and wintering grounds of the Norwegian and Icelandic herring stock (Foote *et al.* 2010). Similar behaviour has been observed for North Atlantic humpback whales (Palsbøll *et al.* 1997), one of the most extensively studied cetacean populations in the world (Smith & Pike, 2009). North Atlantic killer whales and North Atlantic humpback whales both converge to Northern Norway to feed on the Norwegian Spring Spawning (NSS) herring (*Clupea harengus*) every winter season between October and January (Similä et al. 1996, Jourdain & Vongraven, 2017).

Since the 1950s, the NSS herring has established various overwintering areas between the west coast of Iceland and the Norwegian Sea (Huse *et al.* 2010), and from 2015 on it has used the Troms region in Northern Norway (Slotte *et al.* 2015, Salthaug *et al.* 2020). While killer whale distribution in Northern Norway has been known to correlate with the presence of NSS herring (Similä & Ugarte, 1993), humpback whales had not been observed in the previous herring wintering grounds before 2010 (Jourdain & Vongraven, 2017). Most recorded interactions between killer whales and humpback whales are antagonistic (Pitman *et al.* 2017), but Jourdain & Vongraven (2017) have reported the first accounts of feeding aggregations formed by the two species, preying on herring in Northern Norway.

Phylogenetic analysis based on whole mitochondrial genome sequencing has been proven to show more reliable results than the use of short mtDNA fragments (Duchêne *et al.* 2011). Even though cetacean phylogenetic research has relied heavily on regions such as the cytochrome b (CytB) and the control region (CR) (Xiong *et al.* 2009, Morin *et al.* 2010), developments in molecular biology technology have rendered the sequencing of full mitogenome more easily achievable, providing more trustworthy results and allowing interpretations (Duchêne *et al.* 2011).

With the aim of contributing to the current body of knowledge on the biology of killer whales and humpback whales, this study attempts to place the groups that migrate to Northern Norway every year to feast on NSS herring in a global phylogenetic context. To investigate this, phylogenetic trees and haplotype networks were constructed using complete mitochondrial genomes. In addition, this study attempts to identify potential groups or ecotypes, within these individuals and with populations from the whole globe, previously described in literature, which could help shed light on the structure of the North Atlantic populations of killer whales and humpback whales.

3 Materials and Methods

3.1 Sampling area and collection

Tissue samples from free-ranging killer whales (n=151) and humpback whales (n=126) were collected using remote biopsy sampling, during the seasons of 2015/2016, 2016/2017, 2017/2018 and 2018/2019, lasting typically from November to January. Sampling occurred in several areas off the Northern Norwegian coast and adjacent waters, concentrating on the Troms region (**Figure 1**). After the samples were collected, the tissue was divided into skin and blubber. The skin samples were used for this study and were stored at -20°C, either wrapped in aluminium foil or in vials of 96% EtOH. In addition, DNA extracts from killer whales from various areas in the North Atlantic Ocean (n=49), described in Bitz-Thorsen (2017), were included. In total, 200 killer whales (Table S1) and 126 humpback whales (Table S5) were sampled.

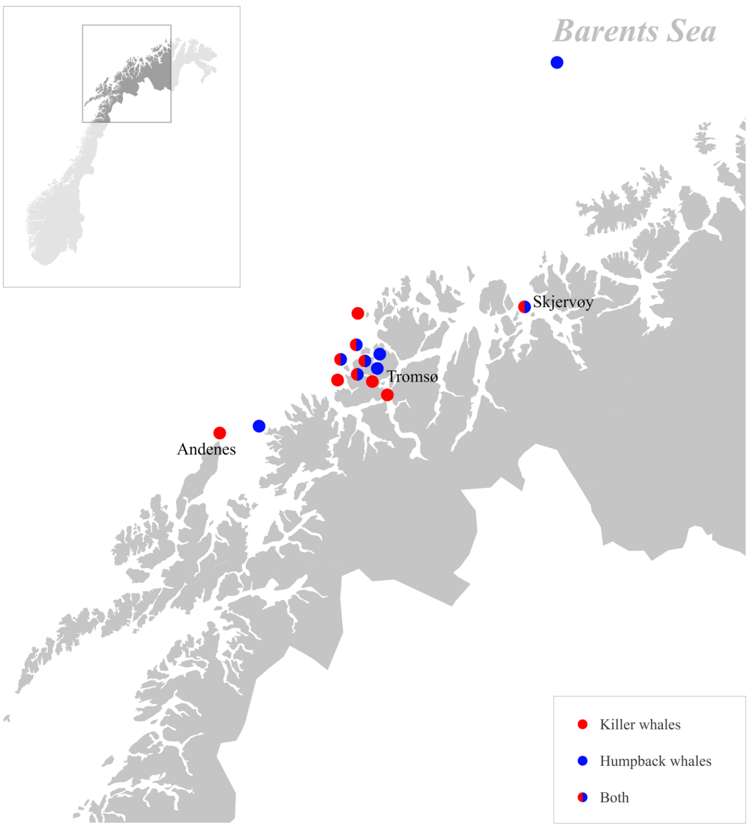

Figure 1: Map over Northern Norway showing approximate sampling locations of killer whales (red dots), humpback whales (blue dots) or both species (bicoloured dots). Samples collected in the Barents Sea were not provided with coordinates, thus that humpback whale sampling location is chosen arbitrarily. The map was acquired in mapsvg.com and edited by Andras Jucksch Ellendersen.

3.2 Molecular techniques

DNA was extracted using the DNeasy Blood and Tissue Kit (Qiagen) following the manufacturer's instructions with minor adjustments. The period of digestion in Proteinase K and ATL buffer was increased to 48 hours, instead of 24 hours. As the skin samples did not dissolve completely, as much as possible of the liquid was transferred into new tubes, avoiding skin fragments, for the ensuing steps in the extraction process. DNA quality was assessed with Gel electrophoresis and concentration was measured with Invitrogen Qubit dsDNA BR (Broad Range) Assay Kit (Thermo Fisher Scientific), or with Invitrogen Quant-iT PicoGreen dsDNA Assay Kit (Thermo Fisher Scientific), averaging around 34,4 ng/µl for killer whales and 51,1ng/µl for humpback whales.

DNA was sheared into fragments of approximate length of 300 bp in Bioruptor (Diagenode) and sequencing libraries were prepared with the NEBNext Ultra DNA Library Prep Kit for Illumina® (New England BioLabs) using the manufacturer's protocol with slight modifications. Quality and size of the libraries were analysed in Agilent 2100 Bioanalyzer (Agilent Technologies). After performing an additional bead cleaning, qPCR analysis was used to check for presence of adaptor-dimers and to quantify library concentration. Each library was pooled into equimolar proportions for each sequencing lane. The pooled samples were shotgun sequenced in four lanes on an Illumina HiSeq4000, using a 150 bp paired end (PE) chemistry, at the commercial sequencing company Novogene (Hong Kong). In total, 178 humpback whale (60 being replicates) libraries and 159 killer whale libraries were sequenced.

3.3 Bioinformatics analysis

FastQC v0.11.4 (Andrews, 2010) and *MultiQC v1.8* (Ewels *et al.* 2016) were used to check for the presence of adapters, bad quality and uncalled bases in the raw data, and to collate all the *FastQC* reports for further visual inspection. The adapters and bad quality bases (q=20) from the raw reads were removed using *cutadapt* (Martin, 2011), using the paired end mode. *GetOrganelle* (Jin *et al.* 2018) was used to assemble the mitochondrial genomes. *GetOrganelle* workflow consists of three overall steps: firstly, the recruiting of organelle-like reads from the dataset using an input seed as initial bait. Herein all the killer whale mitochondrial fragments available on NCBI Genbank were used as seeds, and for humpback whales all the available complete mitogenomes were used. The hitting reads act as further bait to collect more organelle-like reads in multiple iteration steps using *Bowtie2* (Langmead & Salzberg, 2012, Langmead *et al*. 2018). Secondly, all recruited reads from the first step were assembled using different auto-selected k-mer settings in *SPAdes* (Nurk *et al*. 2013). Thirdly, the scaffolds created by *SPAdes* were assigned to taxonomic groups using *Basic Local Alignment Search Tool (BLAST,* Altschul, *et al*. 1990) against an inbuilt *BLAST* library (i.e., collection of animal mitogenomes) to filter out all non-essential scaffolds or contigs, such as nuclear and polymorphic DNA or assembly uncertainties). Only the circularised mitochondrial genomes were kept for further downstream analysis.

Mitogenome sequences were aligned in *Geneious Prime® 2020.0.5*, using the *MUSCLE 3.8.425* (Edgar, 2004) aligner with default settings. In order to maintain a standard start region for the mitogenomes, KR180367 (Morin *et al*. 2015) was used as a reference for killer whales and NC_006927.1 (Sasaki *et al*. 2005) for humpback whales. Once the mitogenomes were aligned and adjusted for read orientation (forward and reverse), the references were removed and the mitogenomes were realigned. All the base polymorphisms were inspected visually to ascertain their validity. In ambiguous regions with variable polynucleotide repeats, where the alignment was considered unreliable, a fixed number of bases was determined, as done in Morin *et al.* (2010), based on the most frequent haplotype among the individuals, in order to avoid introducing false variation into the phylogenetic analysis. For the region between positions 1125 and 1140 in killer whale sequences, three Cs, one A and 12 Cs were settled on. For the region between positions 1791 and 1810 in humpback whale sequences, nine As and eleven Gs were settled on. When certain polymorphisms were represented by a single individual, raw data from that individual was mapped against the reference mitogenome to verify coverage, to rule out polymorphism arising due to sequencing errors. In addition, 60 samples from humpback whales were replicated and used to determine whether they produced same haplotype, showing an error rate of ~0,0003%. The final aligned sequences consist of 134 killer whale samples and 94 humpback whales.

3.4 Phylogenetics and haplotype network analysis

To construct phylogenetic trees and haplotype network, two data sets for each species were prepared. The first one, called the local dataset, is composed solely of the samples sequenced in this study. The second one, called the global dataset, comprises the data generated in this study supplemented with all available full mitogenome haplotypes for both the species: 146 for killer whales (**Table S3**) and three for humpback whales (**Table S7**), acquired from the NCBI GenBank. Due to the scarcity of full mitogenomes of humpback whales, the control region (CR) sequences for this species were downloaded and used in this study (**Table S8** and **Table S9**). To include as many geographically dispersed samples as possible in this study, the mitogenomes sequenced herein were trimmed down to 172 bp (the minimum sequence size in NCBI GenBank) and used for rest of the analysis. All the datasets were aligned using the *MUSCLE* algorithm in *Geneious Prime® 2020.0.5*, with default settings. Haplotype networks were constructed in *PopART* (Leigh & Bryant, 2015) using the Minimum Spanning network inferring method in default settings.

Only unique haplotypes were kept for the phylogenetics analysis (duplicate sequences were removed). The nucleotide substitution model for both the species were determined using command line version of *jModelTest* (Posada, 2008) using default model testing conditions. BIC, AIC, AICc and Decision Tree were used, and the best model was selected based on highest score (**Table 1**). HM060332.1 (*Pseudorca crassidens*), HM060333.2 (*Globicephala macrorhynchus*) and HM060334.1 (*Globicephala melas*), all described in Morin *et al*. (2010) were used as the outgroup for killer whales, and NC_001321.1 (*Balaenoptera physalus*), described in Arnason *et al*. (1991), for humpback whales.

Table 1: Results of the distribution model tests conducted in jModelTest (Posada, 2008). The model holding the highest score is the best fitted model for the given alignment.

Alignment	AIC		AICc		BIC		DT	
	model	score	model	score	model	score	model	score
Killer whales	TIM2	0,132	TIM+I	0,133	HKY	0,863	HKY	0,042
Humpback whales	TIM3+I	0,361	TIM+I	0,362	HKY+I	0,761	HKY+I	0,629

The following analysis was carried out with support from Dr. Shripathi Bhat, RGG, UiT. Bayesian inference based trees were constructed using *BEAST v2.6.2* (Bouckaert et al. 2019). Using *BEAUti v2.6.2* (Bouckaert et al. 2019), XML templates were created, and *BEASTgen v1.0.2* (https://beast.community/beastgen) was used to make input XML files for *BEAST v2.6.2*. Three independent runs were conducted using HKY site model for killer whales and HKY+I site model for humpback whales, with relaxed clock model, Yule model as tree prior, MCMC length between 10,000,000 to 20,000,000 and burn-in of 10%. The convergence of parameters and effective sample size (over 200) for each run were verified visually using *Tracer v1.7* (Rambaut *et al*. 2018). *LogCombiner v2.6.2* (https://beast.community/logcombiner) was used to merge all the trees and log files from the three independent runs into one tree and log file. *DensiTree v2.2.5* (Bouckaert & Heled, 2014) was used to make the final tree by including all the topology and branch uncertainties.

4 Results

4.1 Sequencing and mitogenome assembly

The four sequencing lanes produced 1,713,183,222 PE reads for the killer whale samples and 1,781,057,402 PE reads for the humpback whale samples. 134 full killer whale mitogenomes of ~16390 bp were obtained, with coverage ranging between 17.5x and 558.67x. For humpback whales, 94 full mitogenomes of ~16393 bp were obtained, with coverage varied between 16.74x and 544.81x.

4.2 Killer whales

4.2.1 Phylogenetic analysis

Phylogenetic analysis of the 134 complete killer whale mitogenomes sequenced in this study has identified 19 haplotypes (**Table S2**). The local killer whale phylogenetic tree, including only these unique haplotypes (**Figure 2**), shows three main clades, and haplotype 17 (Oorca16070, from the Shetland Islands) standing alone. The first grouping (haplotypes 1, 3, 9, 10, 15, 16, 18), at the top of the tree, includes the other two Shetland Islands individuals (Oorca16069 and Oorca16072) and Norwegian samples. The second grouping of seven haplotypes (2, 4, 6, 11, 13, 14 and 19) includes the Danish individual (Oorca16073) and the Faroese individual (Oorca16056), sharing haplotype with Norwegian whales. The bottom clade of four haplotypes (5, 7, 8, and 12) consists only of individuals sampled in Greenland.

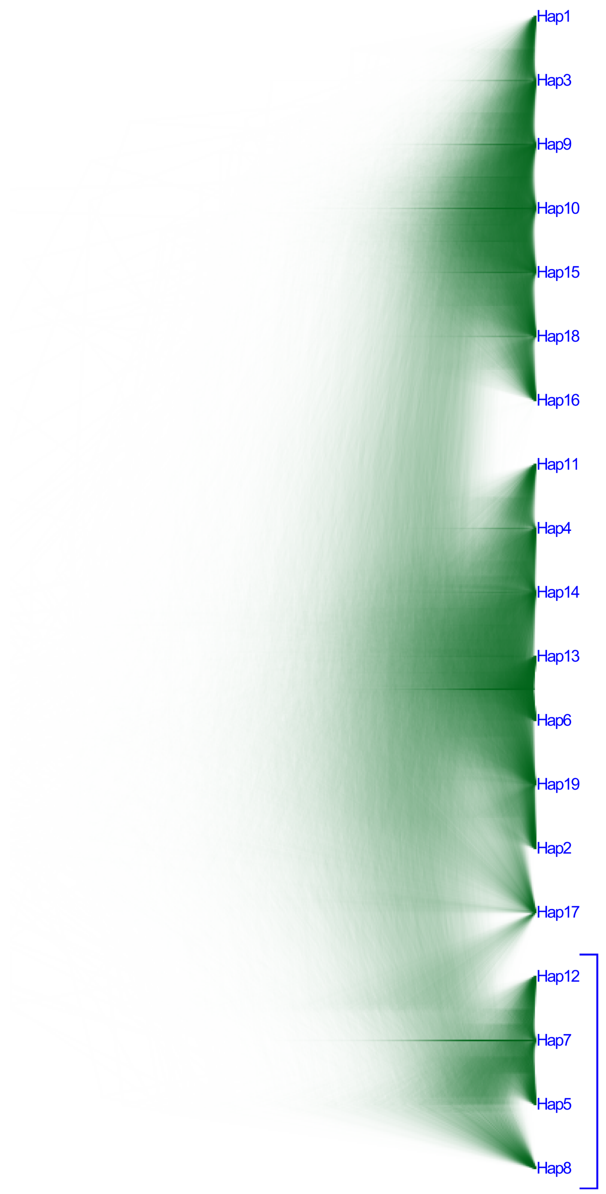

***Figure 2**: Phylogenetic tree of the 19 unique haplotypes identified amongst killer whales of the local dataset. The bracket indicates the Greenlandic clade.*

In order to set the local dataset in a global context, 146 complete killer whale mitogenomes available on NCBI GenBank were added to build a global phylogenetic tree. This tree is shown in figure 3 and reveals four major clades. All the individuals from the local dataset are clustered together in one large clade, that also includes other northern Atlantic individuals. This clade will hereafter be referred to as the Northern North Atlantic (NNA) group.

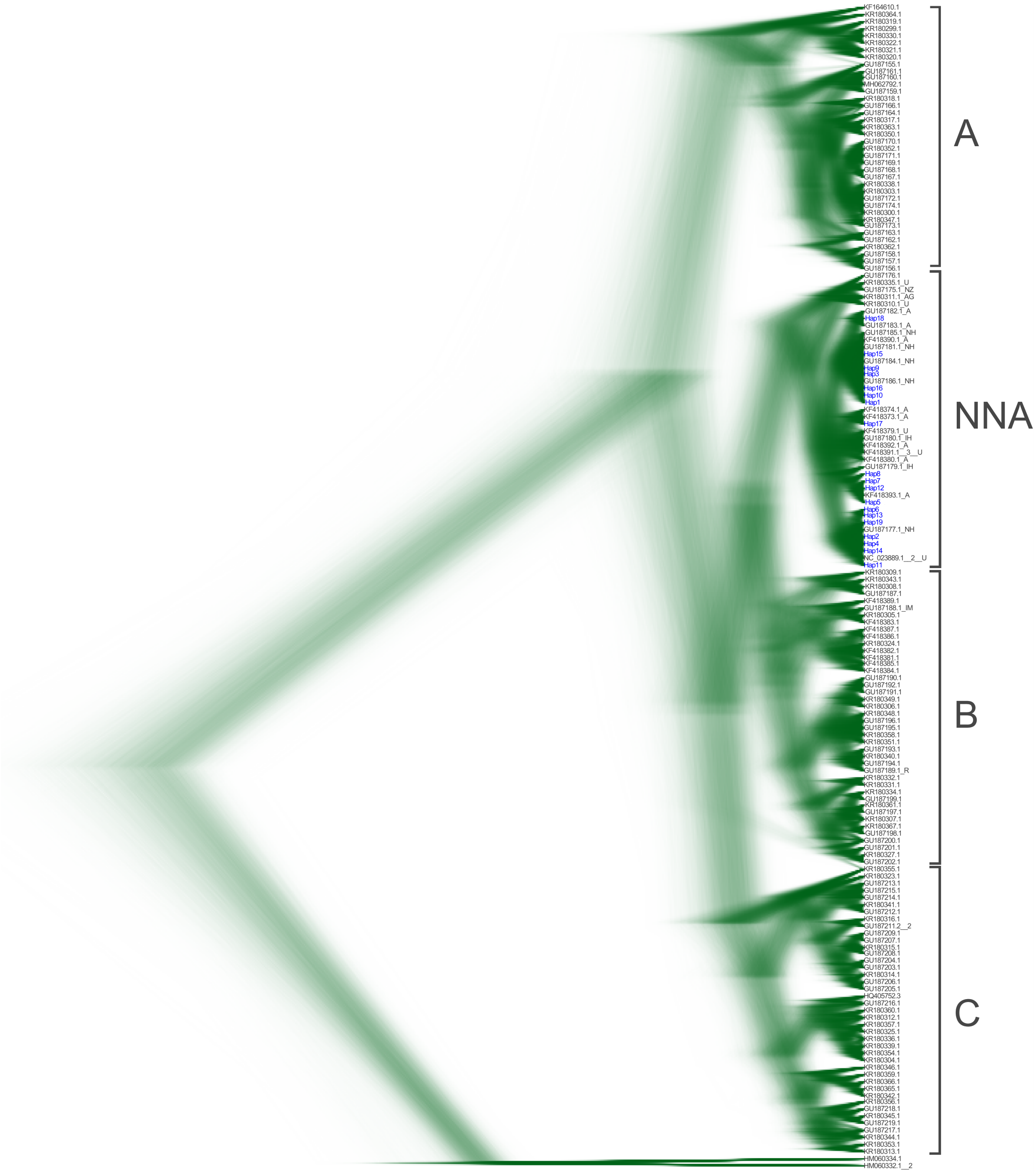

Figure 3*: Global phylogeny of killer whale complete mitogenomes showing four major clades: A,B, C and NNA (Northern North Atlantic), which indicates the clade where all the local killer whale haplotypes are clustered. These are identified in blue by Hap1-Hap19, and additional NCBI GenBank haplotypes are identified in grey by accession numbers. Letters at the end of accession numbers stand for location and sometimes diet information: A: Atlantic; AG: Atlantic-Gibraltar; IH: Iceland-herring; IM: Iceland-mackerel; NH: Norway-herring; NZ: New Zealand; U: unknown. For the outgroup, at the bottom, samples HM060332.1 (*Pseudorca crassidens*), HM060333.2 (*Globicephala macrorhynchus*), HM060334.1 (*Globicephala melas*) were used, all described in Morin* et al. *(2010).*

A phylogenetic tree only containing the NNA killer whale clade, identified in the global phylogeny (**Figure 3**), can be seen in figure 4. The grouping of five haplotypes immediately above the NNA clade is used here as an outgroup, and six main clades are defined (1-6). The four Greenlandic haplotypes (5, 7, 8 and 12) are grouped in clade 1 with samples KF418393.1, sampled off the Shetland Islands, Scotland, and GU187179.1, sampled in Iceland. Clade 2, where local haplotypes 2, 4, 6, 11, 13, 14 and 19 cluster, also includes GU187177.1 and GU187178.1, both of which were sampled in Norway. Haplotype 17, placed alone in the local killer whale phylogenetic tree (**Figure 2**) is here placed in clade 3 with two individuals from Shetland Islands. Clade 4 consists of NCBI GenBank samples from Iceland and the North Sea, and no local individuals. Norwegian haplotype 18 is clustered with three samples from Norway (GU187181.1-GU187183.1), two specifically from Lofoten, in clade 5. Haplotypes 1, 3, 9, 10, 15 and 16 are grouped with samples from Norway and the North Sea, forming clade 6.

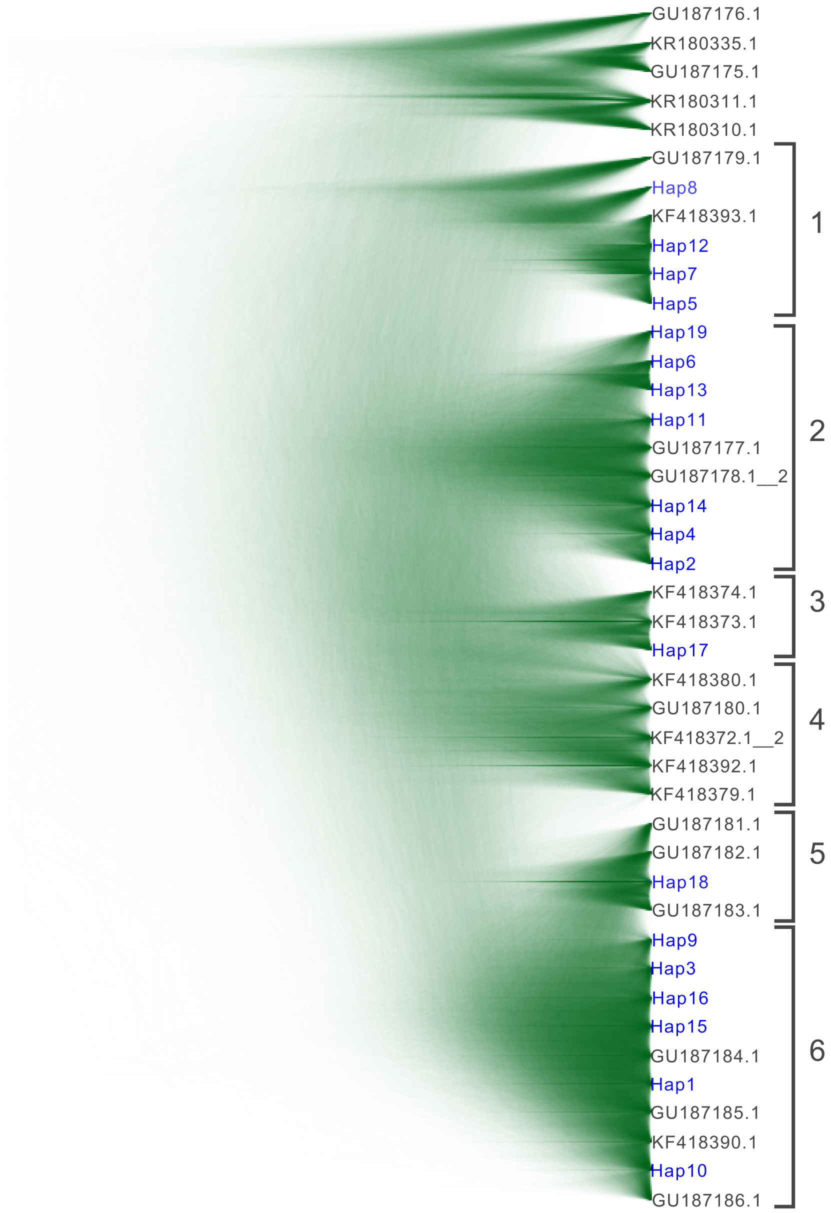

Figure 4*: Phylogenetic analysis of the killer whale NNA group from the global phylogeny analysis revealed six main groupings (clades 1-6). Local haplotypes are identified in blue by Hap1-Hap19 and additional NCBI GenBank haplotypes are identified*

in grey by accession numbers. Accession numbers followed by "_2" indicate that haplotype is shared by one more individual. The top five haplotypes without a bracket form the outgroup.

4.2.2 Haplotype networks

The global killer whale haplotype network (**Figure 5**) revealed that all local samples grouped in one cluster in the bottom left corner (highlighted by the light grey shaded area in **Figure 5**). They were connected to the rest of the world's haplotypes through one individual from the Strait of Gibraltar (GU187176.1, Morin *et al*. (2010)). The cluster also contained other Norwegian individuals, as well as Icelandic ones and individuals labelled as Atlantic, and notably, one individual sampled in New Zealand. This cluster includes all the individuals present in the NNA group phylogenetic tree (**Figure 4**).

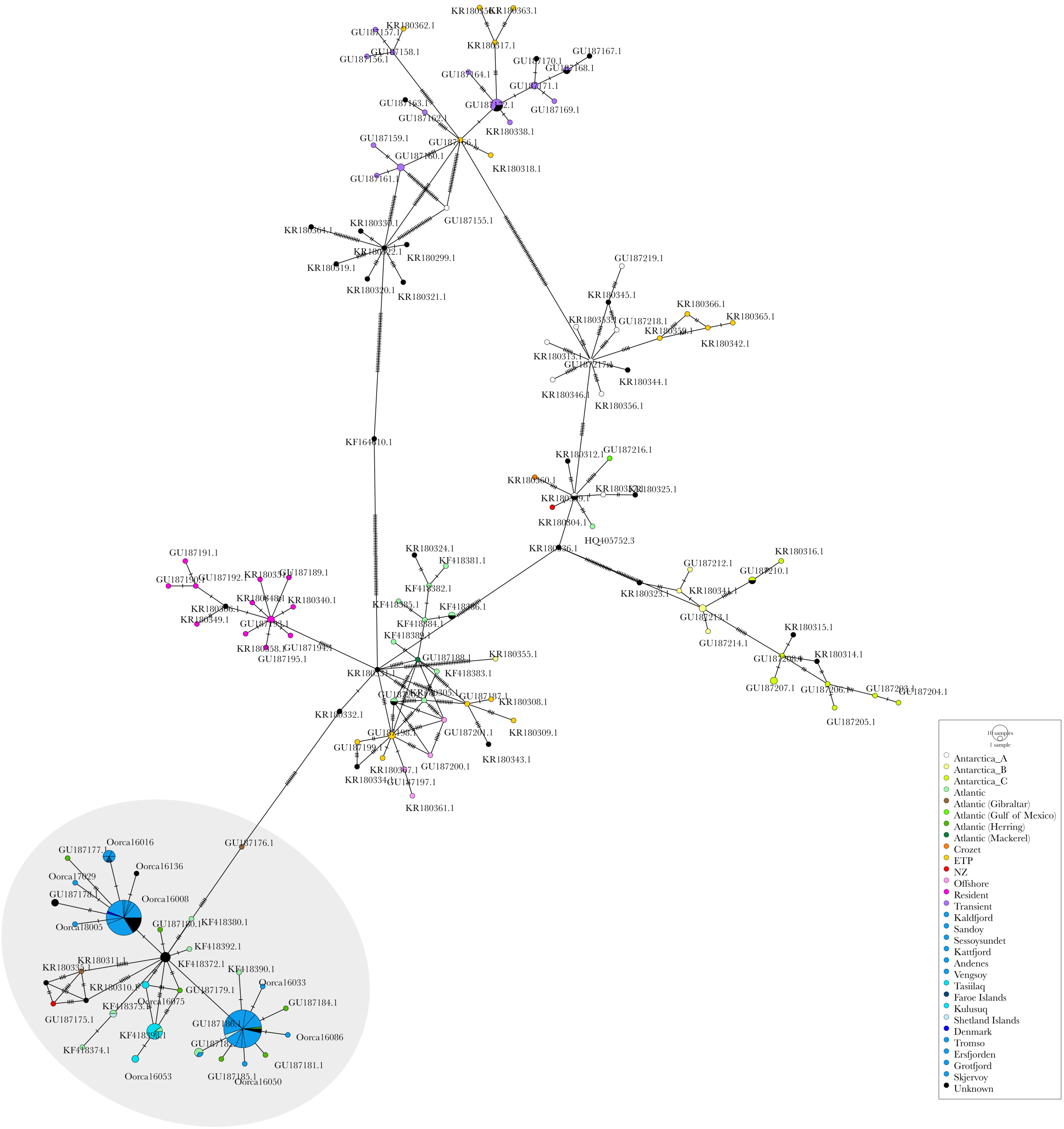

Figure 5: *Global haplotype network of killer whale complete mitogenomes, showing local samples clustered in the shadowed area. The size of the circles reflects the amount of samples sharing the particular haplotypes, and colours represent different sampling locations (in case of local samples) or ecotype-region (in case of the remaining samples), indicated in the legend. The dashes in the lines denote the amount of mutations between sequences. The For the sake of simplicity, all the Norwegian samples of the local dataset have been assigned the same shade of blue. Information on ecotype-region was obtained in the supplementary material of Morin et al. (2010) and Morin et al. (2015). Sequences where that parameter was unclear were considered to be of unknown ecotype-region.*

An additional, more localized haplotype network, built using only haplotypes clustered in the NNA group, revealed that most of the local Norwegian samples were clustered in two main haplotypes, while the Greenlandic samples (from Tasiilaq and Kulusuk) clustered separately (**Figure 6**).

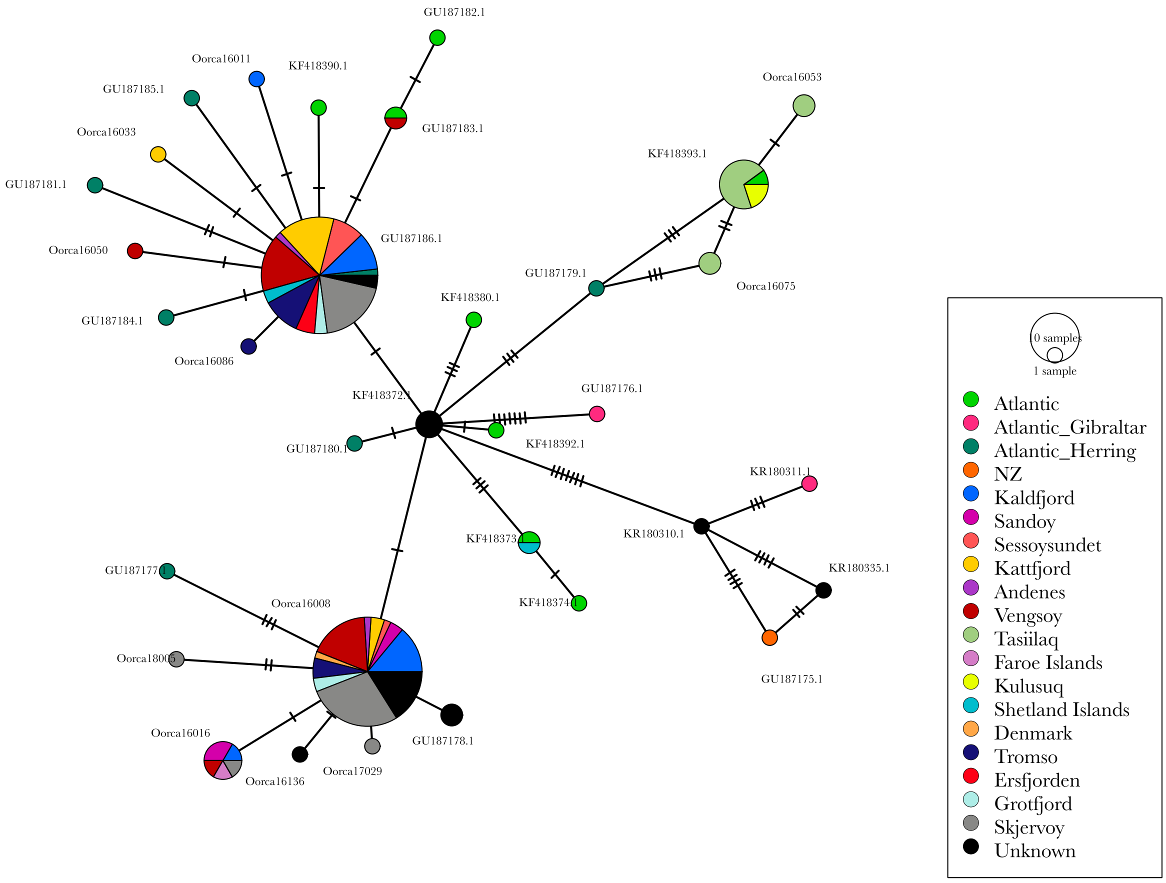

***Figure 6**: NNA killer whale haplotype network. The size of the circles reflects the amount of samples sharing the particular haplotypes, and colours represent different sampling locations (in case of local samples) or ecotype-region (in case of the remaining samples), indicated in the legend. The dashes in the lines denote the amount of mutations between sequences.*

4.3 Humpback whales

4.3.1 Phylogenetic analysis

Unlike the local killer whale samples, which included individuals from other areas of the Northern North Atlantic Ocean, the local humpback whale dataset comprised solely sequences from individuals sampled in Northern Norway. Among the 94 local samples in the final alignment, 18 unique haplotypes were identified (**Table S6**). The resulting phylogenetic analysis of these haplotypes revealed three main groups (**Figure S1**), where haplotype 4 stands separately at the top, followed by a clade formed by haplotypes 1, 6, 14, 15, 16, 17 and 18, a smaller clade consisting of haplotypes 3, 7 and 8, and lastly a clade consisting of haplotypes 2, 5, 9, 10, 11, 12, and 13.

The only other three complete humpback whale mitogenomes available on GenBank were added to the local dataset, in an attempt to identify the placement of the Norwegian humpback whales in the global phylogeny of the species (**Figure 7**). The low amount of additional haplotypes only resulted in a few changes in the structure of the phylogenetic tree. Sample MF409246.1 (Árnasson *et al*. 2018) is situated in the clade with local haplotypes 1, 6, 14, 15, 16, 17 and 18 in clade 1, haplotypes 3, 7 and 8 form clade 2, haplotypes 2, 5, 9, 10, 11, 12 and 13 for clade 3 and NC_006927.1 (Sasaki *et al*. 2005) and AP006467.1 (Sasaki *et al*. 2005) form clade 4 with haplotype 4.

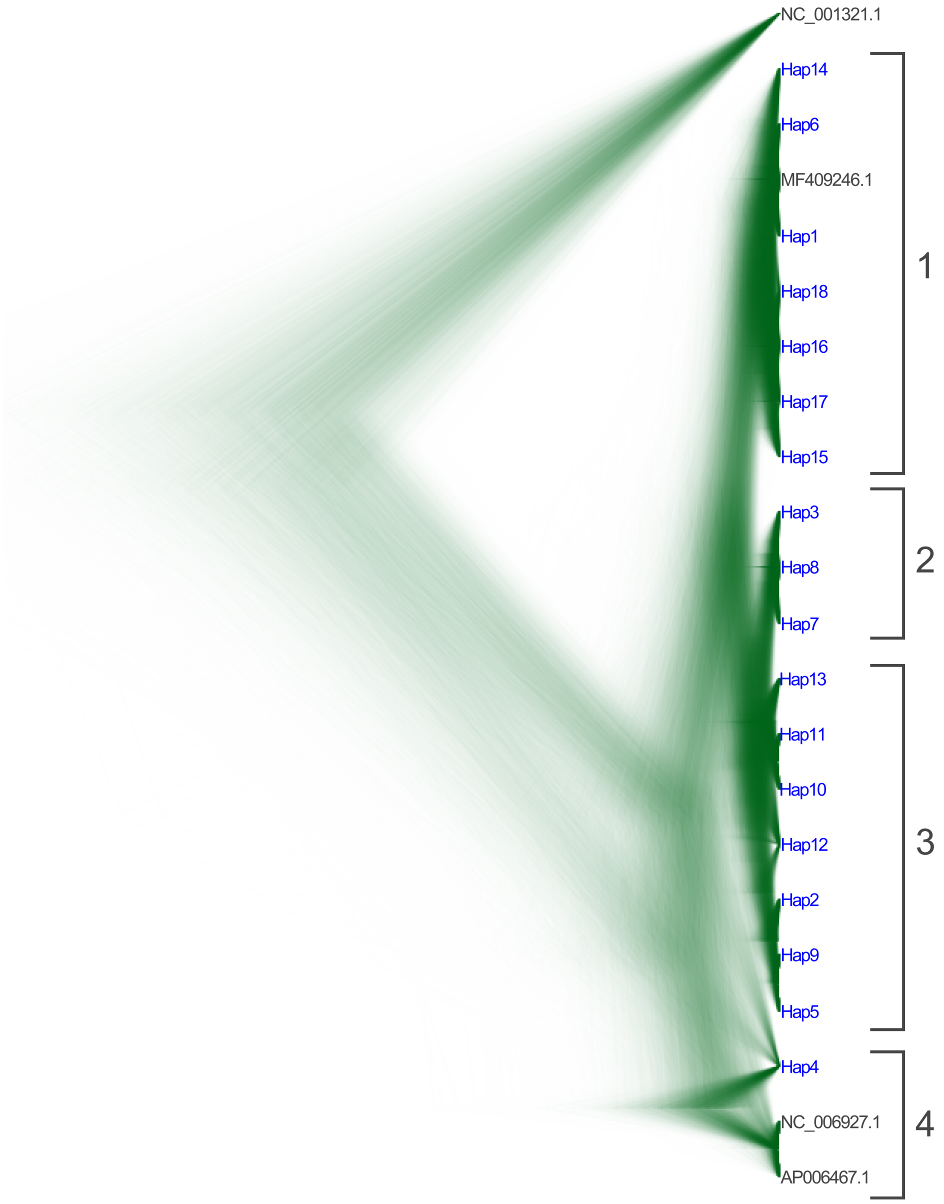

Figure 7: *Global complete mitogenome humpback whale phylogeny, showing four main groups (clades 1-4). Local haplotypes are identified in blue by Hap1-Hap18 and additional NCBI GenBank haplotypes are identified in grey by accession numbers. A fin whale complete mitogenome (NC_001321.1, top of three) was used as outgroup.*

In an effort to get a better understanding of the position of local samples hold relative to humpback whales from other locations, 125 unique haplotypes of humpback whale control region accessible on NCBI GenBank were added to the local dataset. Based on the control region fragment settled on, only eight unique local haplotypes were identified. The resulting phylogenetic tree can be seen on **figure 8**, displaying six main groups (clades A, B, C, D, E and F). Mnova16021 is the only local haplotype situated in clade A, with individuals from Brazil, the Southern Ocean and Western South Pacific. Clade B includes individuals from Eastern

Australia, Antarctica area I, Western South Pacific and Brazil. Clade C embraces samples from Brazil, Southern Ocean and Western South Pacific, and clade D includes samples from those same areas in addition to five haplotypes from Alaska, USA. Clade E includes all the remaining local haplotypes, clustered with individuals from Brazil, Eastern Australia, Southern Ocean and Western South Pacific. Clade F consists primarily of Brazilian samples.

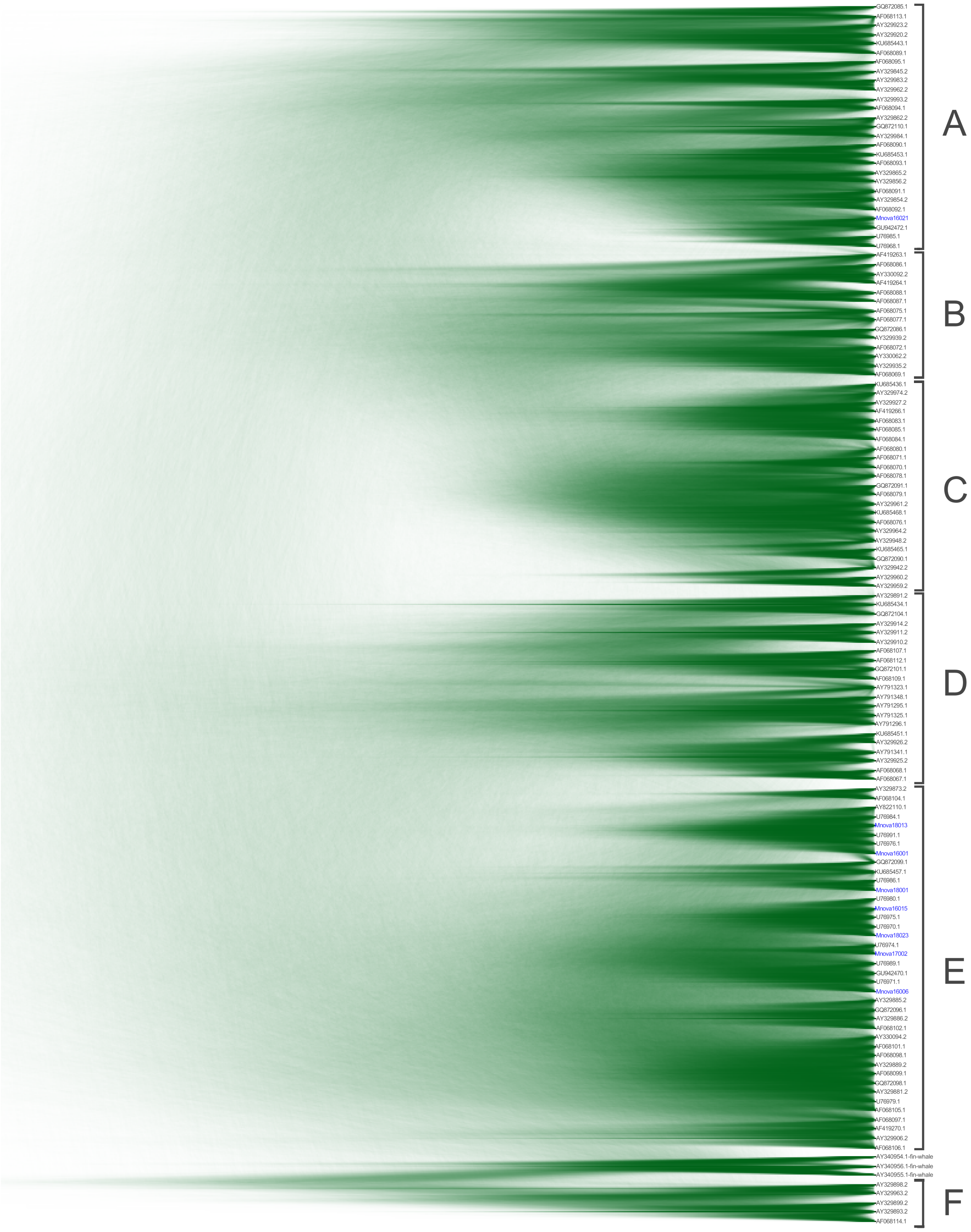

Figure 8*: Global phylogeny of humpback whale control region (CR) showing six main clades (A-F). Local haplotypes appear in blue, identified by sample names starting with Mnova, while additional NCBI GenBank haplotypes are identified in grey by*

accession numbers. Main groups are identified with brackets. The three fin whale samples (AY340954.1, AY340955.1 and AY340956.1) without a bracket were used as the outgroup.

4.3.2 Haplotype networks

The global humpback whale haplotype network encompassing all complete mitogenomes available (local samples and three others acquired on NCBI GenBank) revealed that most local individuals are divided into two main groupings of haplotypes (Figure 9). All of 49 local samples share the haplotype of MF409246.1, described in Árnasson *et al*. (2018), and the other consisted of 18 individuals that gave rise to a previously undescribed haplotype. In addition, nine local individuals have new, unique haplotypes, while smaller groups of 2 to 5 shared haplotypes were also identified. Notably, the four individuals sharing haplotype 4 (identifiable by the sample name Mnova16021) are situated halfway between all the North Atlantic samples and one haplotype from Antarctica (AP006467.1).

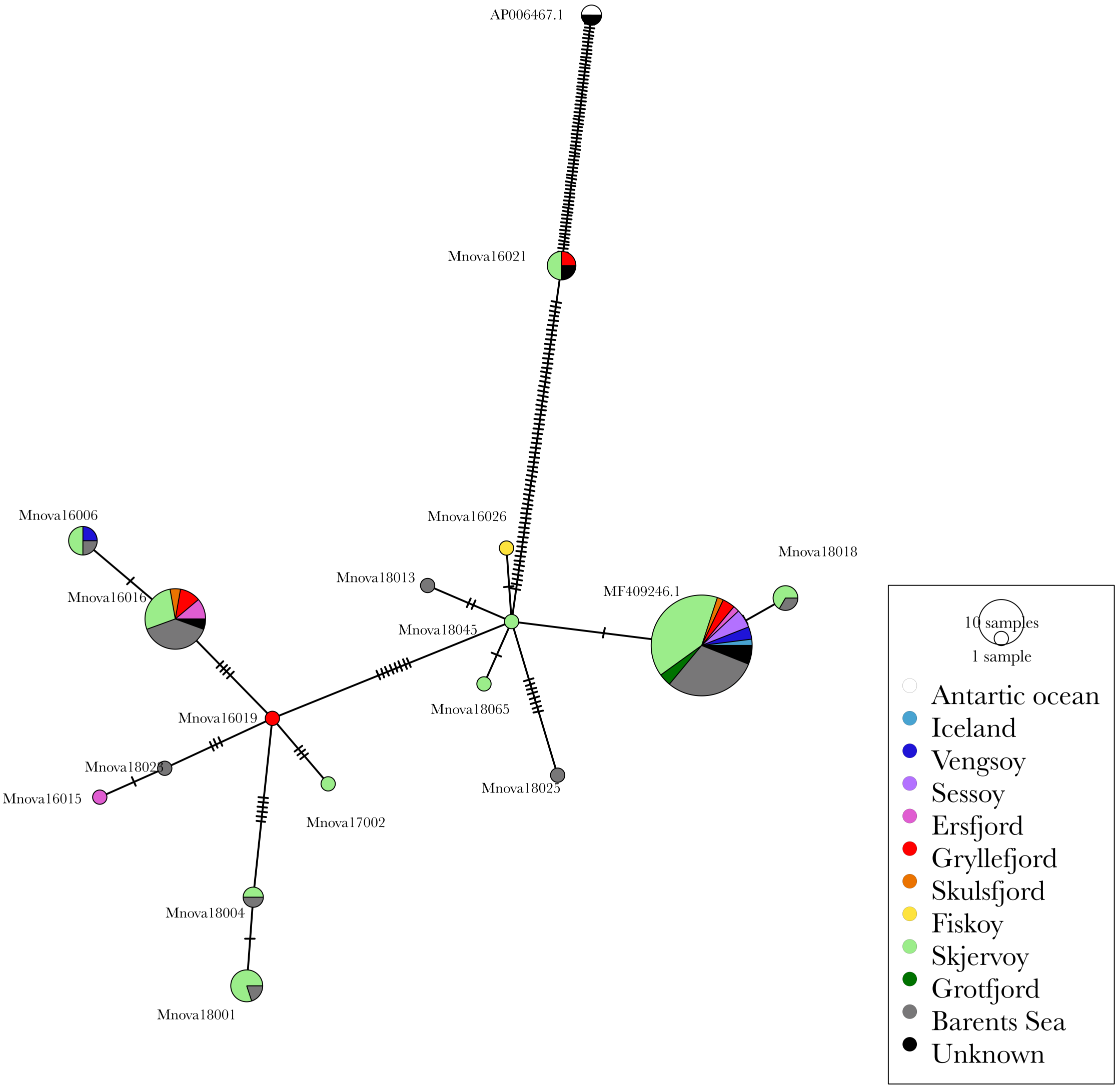

Figure 9: *Global haplotype network of humpback whale complete mitogenomes. The size of the circles reflects the amount of samples sharing the particular haplotypes, and colours represent different sampling locations indicated in the legend. The dashes in the lines denote the amount of mutations between sequences.*

The haplotype network of humpback whale control regions (**Figure 10**) showed a more complex pattern than the global haplotype network of complete mitogenomes (**Figure 9**), with multiple interconnections between haplotypes. Local samples are still grouped closely together, concentrated in two main haplotypes, in a large cluster where a haplotype from Antarctica area I (AY330094.2) is central. The same four samples sharing a haplotype close to Antarctica samples in **figure 9** are consistently placed here quite far from the rest of the local samples, surrounded mainly by Brazilian samples, and close to Southern Ocean, Western South Pacific and Antarctica samples.

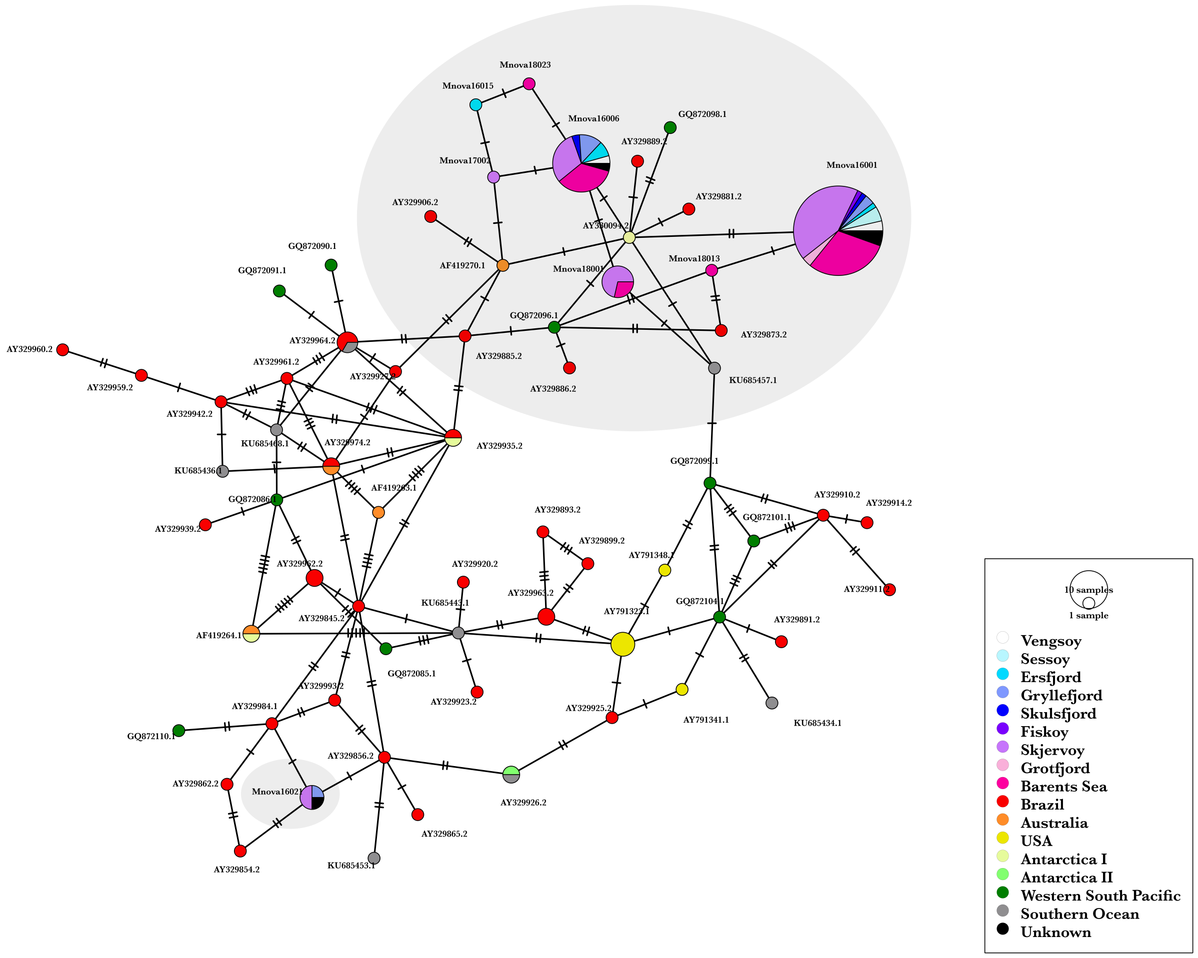

Figure 10: *Global haplotype network of humpback whale control regions of the mitogenome. Shaded areas indicate where the local haplotypes. The dashes in the lines denote the amount of mutations between sequences.*

5 Discussion

Killer whales (*O. orca*) and humpback whales (*M. novaeangliae*) have been observed in the Troms area since 2010 (Jourdain & Vongraven, 2017), feasting on NSS herring (*C. harengus*). To understand the phylogenetic placement of these "Norwegian" whales in a global perspective, the complete mitogenomes of killer whales and humpback whales were used to build phylogenies and haplotype networks with additional data, available in NCBI GenBank, from all over the globe. This study identified 19 haplotypes from 134 killer whale samples and 18 from 94 humpback whale samples, based on complete mitogenome sequences. It also revealed low intraspecific genetic variation within both killer and humpback whales sampled in Northern

Norway, as, for example, killer whale haplotype 1 is shared by 40 samples (**Table S2**), and humpback whale haplotype 1 is shared by 49 (**Table S6**).

Whole mitochondrial genome sequencing of multiple samples, with advances in next generation sequencing, has only recently become a feasible possibility, due to previous prohibitive costs (Duchêne *et al.* 2011). Thus, the majority of currently available data on cetacean phylogeny is based on the analysis of short mitochondrial fragments, notably the CytB (cytochrome b) and the CR (control region) (Xiong *et al.* 2009, Morin *et al.* 2010). The cetacean CR, however, has previously been shown to produce incongruent results, with reports of deceivingly low variation in sperm whales (Alexander *et al.* 2012), and of lack of phylogenetic information leading to misrepresentative phylogeographic interpretations in killer whales (Morin *et al.* 2010). Duchêne *et al.* (2011) additionally proved that partitioning strategies, even using informative genes, fail to produce results comparable to those of full mitogenome analysis.

5.1 Killer whales

The Norwegian killer whales sampled and sequenced in this study show a clear structuring among individuals (Figure 2), and in the global phylogeny are all placed in the NNA clade, with other individuals previously placed in the ecotype ENA type 1. The local killer whales are evidently known to feed on NSS herring (Similä *et al.* 1996), but there are records of other kinds of prey being consumed in Northern Norway (Cosentino, 2015), which is consistent with the ENA type 1 individuals presenting a generalist diet.

The individuals from Greenland, sampled in Tasiilaq and Kulusuk, divided into four haplotypes, and all had seal meat identified in their stomach content (Bitz-Thorsen, 2017), which is supported by blubber fatty acid signature analysis performed in Bourque *et al.* (2018), who identified marine mammals as an important component of Greenlandic individuals. This is also consistent with finds by Foote *et al.* (2013), who identified remains of harp seals (*Pagophilius groenlandicus*) and hooded seals (*Cystophora cristata*) in the stomach content of killer whales sampled off Ammasalik, in the same area of East Greenland. Still, these seal-eating individuals presented tooth wear patterns observed in fish-eating whales, and were furthermore "unambiguously assigned […] to a population consisting mainly of herring-eating killer whales distributed from Norway to Iceland" based on microsatellite allele frequencies (Foote *et al.* 2013). There was no information on whether stomach contents of the Greenlandic killer whales used in this study consisted exclusively on seals, nor is there on data on tooth wear, making it problematic to ascertain if they are generalists or specialists. In addition, Bourque *et al.* (2018) also suggests that dietary variation may occur between individuals within a single pod, possibly even showing disparity between female and male individuals. In the NNA phylogenetic tree (**Figure 4**), the four Greenlandic haplotypes are grouped in clade 1 with samples KF418393.1, from off the Shetland Islands, Scotland, and GU187179.1, from Iceland. This indicates that the Greenlandic individuals are more closely related to individuals from further south than to those feeding on herring in Northern Norway.

Clade 2 includes seven local haplotypes and two NCBI GenBank samples from Norway, making this an almost exclusively Norwegian clade, except for the Danish individual sharing haplotype 2 with 38 Norwegian samples and the Faroese individual sharing haplotype 6 with four. It has recently been suggested that marine mammals are not an essential or even present component of the diet of killer whales from Denmark and the Faroe Islands (Bourque *et al.* 2018), which would validate the position of these two individuals close to herring-eating Norwegian killer whales in this study. Block & Lockyer (1988), while concluding fish to be the main dietary component of killer whales in Faroese waters, compiled extensive records of individuals and groups feeding on a variety of sea bird species, seals, and less often on other cetaceans, such as a harbour porpoise (*Phocoena phocoena*) and a fin whale (*Balaenoptera physalus*). In Foote et al. (2009), however, the four Faroese individuals sampled presented one of the two haplotypes associated with specialist ENA type 2, which is suggested to feed mainly on other cetaceans, affirming the need of further research to solve the Faroese killer whale diet. The Danish sample was acquired from an animal stranded in Western Denmark (Bitz-Thorsen, 2017), which could indicate some relation to other individuals that have been sampled in the North Sea, between Denmark and Shetland Islands.

Haplotype 17, consisting of only one individual from the Shetland Islands (Oorca16070), was placed alone in the local killer whale phylogenetic tree (**Figure 2**) and is located in clade 3 with one individual from Shetland Islands, and one sampled between the same archipelago and Denmark. The other two samples from the Shetland Islands sequenced in this study, one collected on the same day and the other two days before Oorca16070, are notably placed in clade 6 with Norwegian haplotypes, two NCBI GenBank samples from Norway and two from the North Sea. The disparate grouping of the three Shetland Islands individuals in this study could indicate that they do not share the same dietary specialisation. Foote *et al.* (2009) identified the two different North Atlantic ecotypes so far described (ENA Type 1 and ENA type 2), amongst the Shetland Island individuals used in that study. In addition, Shetland Island killer whales have been shown to display dietary variation (seal-hunting and fish-eating) correlating with different vocal behaviour, either within one population or possibly in two reproductively isolated populations (Deecke *et al.* 2011). However, both these dietary specialisations most likely still fall under ENA Type 1, since ENA Type 2 has been hypothesised to feed mainly on other cetaceans (Foote *et al.* 2009). Haplotype 18, previously grouped with haplotypes 1, 3, 9, 10, 15 and 16 in the local phylogeny (**Figure 2**), was placed in the NNA phylogeny in clade 5 with three GenBank samples from Norway, two of which are from the Lofoten Archipelago.

The small clade neighbouring the NNA group, and used as the outgroup for the NNA phylogenetic tree (**Figure 4**) consists of two individuals from Gibraltar, one from Southern Brazil, one from Argentina and notably one killer whale sampled in New Zealand (GU187175.1), which is supported by Morin *et al.* (2010). While killer whales have, albeit rarely, been documented to undertake long-distance movements (Matthews *et al.* 2011, Durban & Pitman, 2011, Andrews *et al.* 2008), little evidence is available on regular or seasonal migration (Durban & Pitman, 2011). A group of eight killer whales in New Zealand waters has been reported to present size and morphology resembling Antarctic ecotypes, suggesting migration between Antarctica and New Zealand or possibly further, as the group had allegedly "arrived from the North" (Visser, 1999). Repeated sightings suggests that the New Zealand killer whale population is most likely permanently or semi-permanently resident in the area (Visser, 2000), and there seems to be no evidence of migration to the Atlantic Ocean in the literature.

5.2 Humpback whales

Humpback whales similarly show well-defined grouping in the phylogeny of local individuals (**Figure S1**). The addition of the three other full mitogenomes (**Figure 7**) showed an Icelandic individual (MF409246.1) clustering with seven local haplotypes in clade 1 and, notably, haplotype 4 forming clade 4 with two external samples, one of which originates from Antarctica.

The phylogenetic tree based on CR humpback whale sequences depicts six main groups, but shows limited variation between them. All clades include Brazilian individuals, Western South Pacific individuals are present in five out of the six clades, Southern Ocean individuals in four. Eastern Australian samples are found in clade B and E. Antarctic samples, though, are exclusive to clade B, and samples from Alaska, USA are restricted to clade D. Haplotype 4, identifiable by the sample name Mnova 16021, is the only local haplotype in clade A, whereas all the other Norwegian haplotypes clustered in clade E.

Haplotype 4 is, consistently, shown relatively close to one haplotype from Antarctica in the complete mitogenome haplotype network (**Figure 9**), and surrounded by haplotypes from Brazil and the Southern Ocean, with difference of only one or two mutations between haplotypes, in the control region haplotype network (**Figure 10**). Sequencing error was ruled out by the fact that haplotype 4 is shared by four different samples. As stated previously, it is not possible to tell from mitogenomic analysis whether these four samples come from separate individuals. Currently, the global humpback whale population is considered to be divided into three oceanic populations: the North Atlantic, the North Pacific and the Southern Hemisphere (Ruegg *et al*. 2013). Even though North Atlantic humpback whales seem to be more strongly differentiated from those in the North Pacific than from those in the Southern Hemisphere (Baker *et al*. 1993), as of 2013, there seem to be no known migratory routes that would explain contact between individuals from Northern Norway and Brazil. The Norwegian individuals sampled in this study naturally fall under the North Atlantic population, and as such are assumed to migrate from the feeding grounds in Norway to North Atlantic breeding grounds in the Caribbean, or possibly to Cape Verde, another hypothesised breeding area (Ruegg *et al*. 2013). Individuals breeding off the Brazilian coast migrate to feeding grounds in Antarctica (Ruegg *et al*. 2013), with no evidence of mixing of populations from the Northern and Southern hemispheres in the literature.

Considering the low amount of available complete humpback whale mitogenomes, building global phylogenetic trees and haplotype networks with CR sequences was deemed helpful and necessary to fulfil the objective of contextualising the Norwegian haplotypes in the global phylogeny. The figures based on the CR (**Figures 8 and 10**) are naturally more complex than the ones with only full mitogenomes (**Figures 7 and 9**), but they are built on sequences of 172 bp. As aforementioned, phylogenetic analysis on short mitochondrial sequences may lead to equivocal results (Duchêne *et al*. 2011). Consequently, while cautious interpretation of the data generated in this study may give valid insight into the global phylogeny of humpback whales, it is possible that a global haplotype network built with as many complete mitogenomes would look noticeably different, considering the higher phylogenetic resolution. Further whole mitogenome research is therefore essential for a full understanding of the relation of Norwegian humpback whales to other populations.

5.3 Relevance and Future Perspectives

This study has attempted to characterise the populations of killer whales and humpback whales that aggregate in Northern Norway to feast on NSS herring. Killer whales have shown both primarily Norwegian groupings, as well as groups mixing Norwegian haplotypes with samples from other areas of the North Atlantic Ocean. The Greenlandic haplotypes dominate a clade that does not include Norwegian haplotypes. One NCBI GenBank sample from New Zealand stood out by being situated in a small clade neighbouring the NNA (Northern North Atlantic) clade in the global killer whale phylogeny. The identification of groups potentially separated genetically, and for example by diet, such as the Greenlandic haplotypes in this study, could add value to arguments in conservation and management of small groupings. The clustering of one humpback whale haplotype with individuals from the Southern Ocean, Western South Pacific and Brazil could indicate that, at least for humpback whales, the NSS herring wintering ground in Northern Norway represents an attractive feeding site on a global scale.

From mitogenomic analysis alone it is not possible to tell whether all the different samples used in this study originate from distinct individuals. As the sampling of both killer whales and humpback whales was conducted through multiple seasons (between 2016 and 2019), and within each season sampling episodes spanned over a period of four or five months (typically between November and January), it is possible that single individuals have been sampled more than once. To address this issue, and to further add to the understanding of killer whales and humpback whales in Northern Norway, nuclear DNA data can be used for more in-depth analysis of genetic relations between individuals and groups. In addition, photo-ID and tagging information are likewise valuable tools to help determine the destination of these individuals after they leave the Troms area and the Barents Sea.

6 Conclusion

The sequencing and analysing of full mitochondrial genomes from Norwegian killer whales and humpback whales has led to the identification of 19 and 18 haplotypes, respectively. Local killer whales showed clear population structuring and were found to cluster into one single clade in the global phylogeny, with other haplotypes assigned to the ENA type 1 ecotype. Local humpback whales also demonstrate structure between individuals, and placed in a global context revealed a previously unreported connection to haplotypes in the Southern Hemisphere. Overall, these results suggest that the NSS herring overwintering ground in Northern Norway is an important feeding site for killer and humpback whales arriving from various areas in the North Atlantic and possibly the South Atlantic Ocean.

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Supplementary Material

Figure S1: Local humpback whale phylogeny

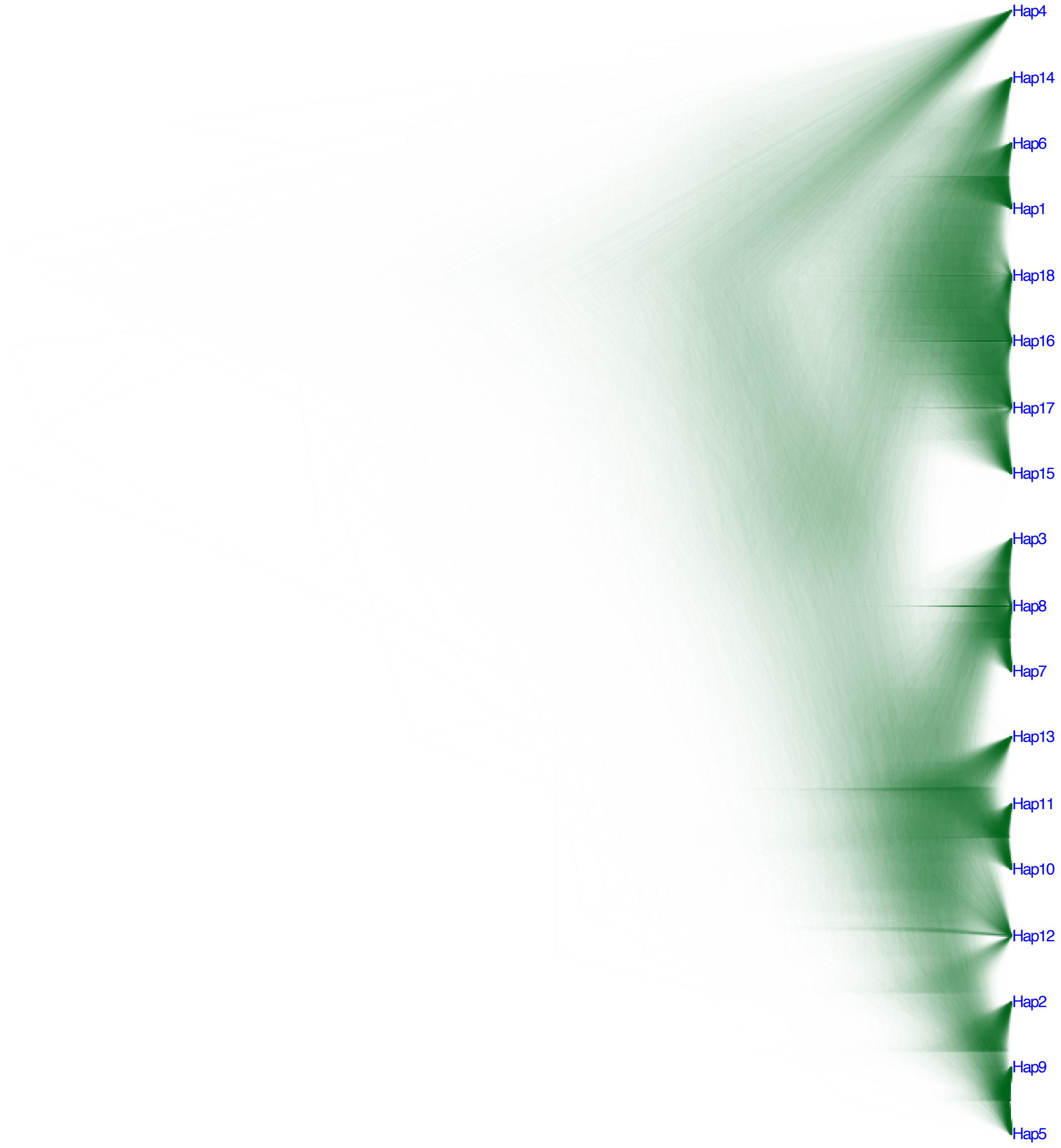

Figure S 1: Phylogenetic tree of the 18 unique haplotypes identified amongst the humpback whales in the local dataset.

Table S1: Killer whale sampling information

Table S 1: Killer whale sample information on date and location of sampling . Shaded Sample IDs were incorporated from Bitz-Thorsen (2017). Samples in red were not used in the phylogenetic analysis.

Sample ID	Date	Location	Sample ID	Date	Location
Oorca16001	03/01/2016	Kaldfjorden	Oorca16101	1/23/2016	Tromsø
Oorca16002	03/01/2016	Kaldfjorden	Oorca16102	06/02/2016	Sessøyfjord

Oorca16003	03/01/2016	Kaldfjorden	Oorca16103	24/01/2017	Ersfjorden
Oorca16004	03/01/2016	Kaldfjorden	Oorca16104	13/01/2017	Grotfjord
Oorca16005	03/01/2016	Kaldfjorden	Oorca16105	24/01/2017	Ersfjorden
Oorca16006	03/01/2016	Kaldfjorden	Oorca16106	26/01/2017	Vengseyfjord
Oorca16007	03/01/2016	Kaldfjorden	Oorca16107	26/01/2017	Vengseyfjord
Oorca16008	05/01/2016	Kaldfjorden	Oorca16108	26/01/2017	Vengseyfjord
Oorca16009	05/01/2016	Kaldfjorden	Oorca16109	26/01/2017	Vengseyfjord
Oorca16010	05/01/2016	Kaldfjorden	Oorca16110	26/01/2017	Vengseyfjord
Oorca16011	05/01/2016	Kaldfjorden	Oorca16111	26/01/2017	Vengseyfjord
Oorca16012	05/01/2016	Kaldfjorden	Oorca16112	03/01/2017	Kaldfjord
Oorca16013	05/01/2016	Kaldfjorden	Oorca16113	26/01/2017	Vengseyfjord
Oorca16014	06/01/2016	Kaldfjorden	Oorca16114	26/01/2017	Vengseyfjord
Oorca16015	06/01/2016	Sandøy	Oorca16115	26/01/2017	Vengseyfjord
Oorca16016	06/01/2016	Sandøy	Oorca16116	26/01/2017	Vengseyfjord
Oorca16017	07/01/2016	Kaldfjorden	Oorca16117	26/01/2017	Vengseyfjord
Oorca16018	07/01/2016	Kaldfjorden	Oorca16118	26/01/2017	Vengseyfjord
Oorca16019	09/01/2016	Sessøysundet	Oorca16119	26/01/2017	Vengseyfjord
Oorca16020	09/01/2016	Sessøysundet	Oorca16120	26/01/2017	Kaldfjord
Oorca16021	09/01/2016	Ersfj/Kattfjord	Oorca16121	26/01/2017	Kaldfjord
Oorca16022	09/01/2016	Kattfjord	Oorca16122	26/01/2017	Vengseyfjord nord
Oorca16023	09/01/2016	Kattfjord	Oorca16123	26/01/2017	Vengseyfjord nord
Oorca16024	09/01/2016	Kattfjord	Oorca16124	03/01/2017	Kaldfjord
Oorca16025	09/01/2016	Kattfjord	Oorca16125	11/12/2016	Ytre Kaldfjord
Oorca16026	09/01/2016	Kattfjord	Oorca16126	11/12/2016	Ytre Kaldfjord
Oorca16027	09/01/2016	Kattfjord	Oorca16127	02/11/2016	
Oorca16028	09/01/2016	Kattfjord	Oorca16128	03/01/2017	Kaldfjord
Oorca16029	17/11/2015	Andenes	Oorca16129	13/01/2017	Grotfjord
Oorca16030	17/11/2015	Andenes	Oorca16130	24/01/2017	Ersfjorden
Oorca16031	17/11/2015	Andenes	Oorca16131	13/01/2017	Grotfjord
Oorca16032	04/01/2016	Kattfjord	Oorca16132	07/11/2016	Sandoya
Oorca16033	04/01/2016	Kattfjord	Oorca16133	02/11/2016	
Oorca16034	04/01/2016	Kattfjord	Oorca16134	07/11/2016	Sandoya
Oorca16035	13/01/2016	Vengsøysundet	Oorca16135	02/11/2016	
Oorca16036	13/01/2016	Vengsøysundet	Oorca16136		
Oorca16037	16/01/2016	Kaldfjorden	Oorca16137	07/11/2016	Sandoya
Oorca16038	17/01/2016	Sessøysundet	Oorca16138	13/01/2017	Grotfjord
Oorca16039	17/01/2016	Sessøysundet	Oorca16139	03/01/2017	Kaldfjord

Oorca16040	17/01/2016	Sessøysundet	Oorca17001	15/11/2017	
Oorca16041	17/01/2016	Sessøysundet	Oorca17002	17/11/2017	Skjervoy
Oorca16042	17/01/2016	Sessøysundet	Oorca17003	15/11/2017	
Oorca16043	17/01/2016	Sessøysundet	Oorca17004	15/11/2017	
Oorca16044	23/01/2016	Kattfjord	Oorca17005	15/11/2017	
Oorca16045	23/01/2016	Kattfjord	Oorca17006	15/11/2017	
Oorca16046	23/01/2016	Kattfjord	Oorca17007	15/11/2017	
Oorca16047	24/01/2016	Kaldfjorden	Oorca17008	15/11/2017	
Oorca16048	28/01/2016	Vengsøyfjorden	Oorca17009	15/11/2017	
Oorca16049	28/01/2016	Vengsøyfjorden	Oorca17010	17/11/2017	Skjervoy
Oorca16050	28/01/2016	Vengsøyfjorden	Oorca17011	17/11/2017	Skjervoy
Oorca16051	28/01/2016	Vengsøyfjorden	Oorca17012	17/11/2017	Skjervoy
Oorca16052	28/01/2016	Vengsøyfjorden	Oorca17013	17/11/2017	Skjervoy
Oorca16053	8/20/2013	Tasiilaq	Oorca17014	17/11/2017	Skjervoy
Oorca16054	8/22/2013	Tasiilaq	Oorca17015	15/11/2017	Skjervoy
Oorca16055	4/14/2008	Faroe Islands, Klarksvik	Oorca17016	15/11/2017	Skjervoy
Oorca16056	4/14/2008	Faroe Islands, Skalavik	Oorca17017	15/11/2017	Skjervoy
Oorca16057	8/21/2012	Tasiilaq	Oorca17018	15/11/2017	Skjervoy
Oorca16058	8/21/2012	Tasiilaq	Oorca17019	15/11/2017	Skjervoy
Oorca16059	8/21/2012	Tasiilaq	Oorca17020	15/11/2017	Skjervoy
Oorca16060	8/21/2012	Tasiilaq	Oorca17021	15/11/2017	Skjervoy
Oorca16061	8/21/2012	Tasiilaq	Oorca17022	22/01/2018	
Oorca16062	8/21/2012	Tasiilaq	Oorca17023	22/01/2018	
Oorca16063	8/21/2012	Tasiilaq	Oorca17024	22/01/2018	Skjervøy
Oorca16064	8/21/2012	Tasiilaq	Oorca17025	22/01/2018	
Oorca16065	9/15/2013	Tasiilaq	Oorca17026	25/10/2017	
Oorca16066	08/12/2013	Kulusuq	Oorca17027	11/01/2018	Skjervoy
Oorca16067	8/13/2013	Kulusuq	Oorca17028	11/01/2018	
Oorca16068	8/14/2013	Tasiilaq	Oorca17029	11/01/2018	Skjervoy
Oorca16069	9/26/2013	Shetland Island	Oorca17030	11/01/2018	Skjervoy
Oorca16070	9/28/2013	Shetland Island	Oorca17031	11/01/2018	Skjervoy
Oorca16071	9/28/2013	Shetland Island	Oorca18001	05/01/2019	Skjervøj
Oorca16072	9/28/2013	Shetland Island	Oorca18002	05/01/2019	Skjervøj
Oorca16073	01/01/2005	Denmark	Oorca18003	28/10/2018	Skjervøy
Oorca16074	8/21/2012	Tasiilaq	Oorca18004	26/10/2018	Skjervøy
Oorca16075	8/15/2014	Tasiilaq	Oorca18005	06/11/2018	Skjervøy
Oorca16076	07/10/2014	Tasiilaq	Oorca18006	06/11/2018	Skjervøy
Oorca16077	7/15/2014	Tasiilaq	Oorca18007	06/11/2018	Skjervøy
Oorca16078	7/20/2014	Tasiilaq	Oorca18008	06/11/2018	Skjervøy

Oorca16079	8/15/2014	Tasiilaq	Oorca18009	06/11/2018	Skjervøy
Oorca16080			Oorca18010	06/11/2018	Skjervøy
Oorca16081			Oorca18011	06/11/2018	Skjervøy
Oorca16082	1/14/2016	Tromsø	Oorca18012	06/11/2018	Skjervøy
Oorca16083	1/14/2016	Tromsø	Oorca18013	06/11/2018	Skjervøy
Oorca16084	1/14/2016	Tromsø	Oorca18014	14/11/2018	Skjervøy
Oorca16085	1/16/2016	Tromsø	Oorca18015	13/11/2018	
Oorca16086	1/19/2016	Tromsø	Oorca18016	13/11/2018	
Oorca16087	1/19/2016	Tromsø	Oorca18017	13/11/2018	
Oorca16088	1/19/2016	Tromsø	Oorca18018	13/11/2018	
Oorca16089	1/19/2016	Tromsø	Oorca18019	15/11/2018	Skjervøy
Oorca16090	1/19/2016	Tromsø	Oorca18020	15/11/2018	Skjervøy
Oorca16091	1/19/2016	Tromsø	Oorca18021	02/12/2018	Skjervøy
Oorca16092	1/20/2016	Tromsø	Oorca18022	02/12/2018	Skjervøy
Oorca16093	1/20/2016	Tromsø	Oorca18023	02/12/2018	Skjervøy
Oorca16094	1/20/2016	Tromsø	Oorca18024	02/12/2018	Skjervøy
Oorca16095	1/20/2016	Tromsø	Oorca18025	02/12/2018	Skjervøy
Oorca16096	1/21/2016	Tromsø	Oorca18026	02/12/2018	Skjervøy
Oorca16097	1/21/2016	Tromsø	Oorca18027	02/12/2018	Skjervøy
Oorca16098	1/21/2016	Tromsø	Oorca18028	23/01/2019	
Oorca16099	1/22/2016	Tromsø	Oorca18029	23/01/2019	
Oorca16100	1/23/2016	Tromsø	Oorca18030	23/01/2019	Skjervøj (?)

Table S2: Killer whale haplotypes

Table S 2: Killer whale samples divided into haplotypes identified in this study.

Sample ID	Location	Haplotype	Sample ID	Location	Haplotype
Oorca16001	Kaldfjord	Haplotype 1	Oorca16026	Kattfjord	Haplotype 3
Oorca16004	Kaldfjord		Oorca16027	Kattfjord	
Oorca16007	Kaldfjord		Oorca16028	Kattfjord	
Oorca16014	Kaldfjord		Oorca16032	Kattfjord	
Oorca16019	Sessoy		Oorca16040	Sessoy	
Oorca16020	Sessoy		Oorca16045	Kattfjord	
Oorca16022	Kattfjord		Oorca16072	Shetland Islands	
Oorca16031	Andenes		Oorca16084	Tromsø	
Oorca16034	Kattfjord		Oorca16103	Ersfjord	
Oorca16041	Sessoy		Oorca16105	Ersfjord	
Oorca16042	Sessoy		Oorca16114	Vengsoy	

Oorca16044	Kattfjord		Oorca16122	Vengsoy	
Oorca16046	Kattfjord		Oorca16123	Vengsoy	
Oorca16047	Kaldfjord		Oorca16130	Ersfjord	
Oorca16049	Vengsoy		Oorca17030	Skjervoy	
Oorca16052	Vengsoy		Oorca18026	Skjervoy	
Oorca16069	Shetland Islands		Oorca16102	Sessøy	Haplotype 4
Oorca16082	Tromsø		Oorca16090	Tromsø	
Oorca16087	Tromsø		Oorca16096	Tromsø	
Oorca16088	Tromsø		Oorca16106	Vengsoy	
Oorca16094	Tromsø		Oorca16113	Vengsoy	
Oorca16095	Tromsø		Oorca16116	Vengsoy	
Oorca16104	Grotfjord		Oorca16133	Unknown	
Oorca16107	Vengsoy		Oorca17002	Skjervoy	
Oorca16108	Vengsoy		Oorca18014	Skjervoy	
Oorca16117	Vengsoy		Oorca18018	Unknown	
Oorca16119	Vengsoy		Oorca18022	Skjervoy	
Oorca16121	Kaldfjord		Oorca18029	Unknown	
Oorca16129	Grotfjord		Oorca16057	Tasiilaq	Haplotype 5
Oorca17001	Unknown		Oorca16061	Tasiilaq	
Oorca17027	Skjervoy		Oorca16062	Tasiilaq	
Oorca17028	Unknown		Oorca16063	Tasiilaq	
Oorca17031	Skjervoy		Oorca16064	Tasiilaq	
Oorca18001	Skjervoy		Oorca16066	Kulusuq	
Oorca18002	Skjervoy		Oorca16068	Tasiilaq	
Oorca18009	Skjervoy		Oorca16074	Tasiilaq	
Oorca18020	Skjervoy		Oorca16016	Sandoy	Haplotype 6
Oorca18024	Skjervoy		Oorca16056	Faroe Islands	
Oorca18025	Skjervoy		Oorca16109	Vengsoy	
Oorca18027	Skjervoy		Oorca16125	Kaldfjord	
Oorca16008	Kaldfjord	Haplotype 2	Oorca18019	Skjervoy	
Oorca16021	Kattfjord		Oorca16053	Tasiilaq	Haplotype 7
Oorca16024	Kattfjord		Oorca16065	Tasiilaq	
Oorca16030	Andenes		Oorca16075	Tasiilaq	Haplotype 8
Oorca16035	Vengsoy		Oorca16079	Tasiilaq	
Oorca16036	Vengsoy		Oorca16050	Vengsoy	Haplotype 9
Oorca16048	Vengsoy		Oorca16011	Kaldfjord	Haplotype 10
Oorca16073	Denmark		Oorca17029	Skjervoy	Haplotype 11
Oorca16085	Tromsø		Oorca16067	Kulusuq	Haplotype 12
Oorca16111	Vengsoy		Oorca16134	Sandoy	Haplotype 13

Oorca16112	Kaldfjord		Oorca16136	Unknown	Haplotype 14
Oorca16115	Vengsoy		Oorca16033	Kattfjord	Haplotype 15
Oorca16118	Vengsoy		Oorca16083	Tromsø	Haplotype 16
Oorca16120	Kaldfjord		Oorca16070	Shetland Islands	Haplotype 17
Oorca16124	Kaldfjord		Oorca16110	Vengsoy	Haplotype 18
Oorca16126	Kaldfjord		Oorca18005	Skjervoy	Haplotype 19
Oorca16127	Unknown				
Oorca16128	Kaldfjord				
Oorca16131	Grotfjord				
Oorca16132	Sandoy				
Oorca16137	Sandoy				
Oorca16138	Grotfjord				
Oorca16139	Kaldfjord				
Oorca18003	Skjervoy				
Oorca18006	Skjervoy				
Oorca18007	Skjervoy				
Oorca18008	Skjervoy				
Oorca18010	Skjervoy				
Oorca18011	Skjervoy				
Oorca18012	Skjervoy				
Oorca18013	Skjervoy				
Oorca18015	Unknown				
Oorca18016	Unknown				
Oorca18017	Unknown				
Oorca18021	Skjervoy				
Oorca18023	Skjervoy				
Oorca18028	Unknown				
Oorca18030	Skjervoy				

Table S3: GenBank killer whale sequences

Table S 3: Killer whale full mitogenomes downloaded from GenBank. Shaded accession numbers fell under the NNA group.

Accession number	Ecotype-region	Source	Accession number	Ecotype-region	Source
GU187155.1	Antarctica_A	Morin et al. 2010	KF418383.1	Atlantic	Foote et al. 2013b
GU187156.1	Transient	Morin et al. 2010	KF418384.1	Atlantic	Foote et al. 2013b

GU187157.1	Transient	Morin et al. 2010	KF418385.1	Atlantic	Foote et al. 2013b
GU187158.1	Transient	Morin et al. 2010	KF418386.1	Unknown	Foote et al. 2013b
GU187159.1	Transient	Morin et al. 2010	KF418387.1	Atlantic	Foote et al. 2013b
GU187160.1	Transient	Morin et al. 2010	KF418389.1	Atlantic	Foote et al. 2013b
GU187161.1	Transient	Morin et al. 2010	KF418390.1	Atlantic	Foote et al. 2013b
GU187162.1	Transient	Morin et al. 2010	KF418391.1	Unknown	Foote et al. 2013b
GU187163.1	Unknown	Morin et al. 2010	KF418392.1	Atlantic	Foote et al. 2013b
GU187164.1	Transient	Morin et al. 2010	KF418393.1	Atlantic	Foote et al. 2013b
GU187166.1	ETP	Morin et al. 2010	KR180299.1	Unknown	Morin et al. 2015
GU187167.1	Unknown	Morin et al. 2010	KR180300.1	Unknown	Morin et al. 2015
GU187168.1	Transient	Morin et al. 2010	KR180303.1	Unknown	Morin et al. 2015
GU187169.1	Transient	Morin et al. 2010	KR180304.1	New Zealand	Morin et al. 2015
GU187170.1	Unknown	Morin et al. 2010	KR180305.1	Atlantic	Morin et al. 2015
GU187171.1	Transient	Morin et al. 2010	KR180306.1	Unknown	Morin et al. 2015
GU187172.1	Transient	Morin et al. 2010	KR180307.1	ETP	Morin et al. 2015
GU187173.1	Transient	Morin et al. 2010	KR180308.1	ETP	Morin et al. 2015
GU187174.1	Transient	Morin et al. 2010	KR180309.1	ETP	Morin et al. 2015
GU187175.1	New Zealand	Morin et al. 2010	KR180310.1	Unknown	Morin et al. 2015
GU187176.1	Atlantic (Gibraltar)	Morin et al. 2010	KR180311.1	Atlantic (Gibraltar)	Morin et al. 2015
GU187177.1	Atlantic (Herring)	Morin et al. 2010	KR180312.1	Unknown	Morin et al. 2015
GU187178.1	Unknown	Morin et al. 2010	KR180313.1	Antarctica_A	Morin et al. 2015
GU187179.1	Atlantic (Herring)	Morin et al. 2010	KR180314.1	Unknown	Morin et al. 2015
GU187180.1	Atlantic (Herring)	Morin et al. 2010	KR180315.1	Unknown	Morin et al. 2015
GU187181.1	Atlantic (Herring)	Morin et al. 2010	KR180316.1	Antarctica_C	Morin et al. 2015
GU187182.1	Atlantic	Morin et al. 2010	KR180317.1	ETP	Morin et al. 2015
GU187183.1	Atlantic	Morin et al. 2010	KR180318.1	ETP	Morin et al. 2015
GU187184.1	Atlantic (Herring)	Morin et al. 2010	KR180319.1	Unknown	Morin et al. 2015
GU187185.1	Atlantic (Herring)	Morin et al. 2010	KR180320.1	Unknown	Morin et al. 2015
GU187186.1	Atlantic (Herring)	Morin et al. 2010	KR180321.1	Unknown	Morin et al. 2015
GU187187.1	ETP	Morin et al. 2010	KR180322.1	Unknown	Morin et al. 2015
GU187188.1	Atlantic (Mackerel)	Morin et al. 2010	KR180323.1	Unknown	Morin et al. 2015
GU187189.1	Resident	Morin et al. 2010	KR180324.1	Unknown	Morin et al. 2015
GU187190.1	Resident	Morin et al. 2010	KR180325.1	Unknown	Morin et al. 2015
GU187191.1	Resident	Morin et al. 2010	KR180327.1	Atlantic	Morin et al. 2015
GU187192.1	Resident	Morin et al. 2010	KR180330.1	Atlantic	Morin et al. 2015
GU187193.1	Resident	Morin et al. 2010	KR180331.1	Atlantic	Morin et al. 2015
GU187194.1	Resident	Morin et al. 2010	KR180332.1	Atlantic	Morin et al. 2015

GU187195.1	Resident	Morin et al. 2010	KR180334.1	Atlantic	Morin et al. 2015
GU187196.1	Resident	Morin et al. 2010	KR180335.1	Atlantic	Morin et al. 2015
GU187197.1	Offshore	Morin et al. 2010	KR180336.1	Atlantic	Morin et al. 2015
GU187198.1	ETP	Morin et al. 2010	KR180338.1	Transient	Morin et al. 2015
GU187199.1	ETP	Morin et al. 2010	KR180339.1	Antarctica_A	Morin et al. 2015
GU187200.1	Offshore	Morin et al. 2010	KR180340.1	Resident	Morin et al. 2015
GU187201.1	Offshore	Morin et al. 2010	KR180341.1	Antarctica_B	Morin et al. 2015
GU187202.1	Unknown	Morin et al. 2010	KR180342.1	ETP	Morin et al. 2015
GU187203.1	Antarctica_C	Morin et al. 2010	KR180343.1	Unknown	Morin et al. 2015
GU187204.1	Antarctica_C	Morin et al. 2010	KR180344.1	Unknown	Morin et al. 2015
GU187205.1	Antarctica_C	Morin et al. 2010	KR180345.1	Unknown	Morin et al. 2015
GU187206.1	Antarctica_C	Morin et al. 2010	KR180346.1	Antarctica_A	Morin et al. 2015
GU187207.1	Antarctica_C	Morin et al. 2010	KR180347.1	Transient	Morin et al. 2015
GU187208.1	Antarctica_C	Morin et al. 2010	KR180348.1	Resident	Morin et al. 2015
GU187209.1	Antarctica_C	Morin et al. 2010	KR180349.1	Resident	Morin et al. 2015
GU187210.1	Unknown	Morin et al. 2010	KR180350.1	ETP	Morin et al. 2015
GU187211.2	Antarctica_C	Morin et al. 2010	KR180351.1	Resident	Morin et al. 2015
GU187212.1	Antarctica_B	Morin et al. 2010	KR180352.1	Transient	Morin et al. 2015
GU187213.1	Antarctica_B	Morin et al. 2010	KR180353.1	Antarctica_A	Morin et al. 2015
GU187214.1	Antarctica_B	Morin et al. 2010	KR180354.1	Unknown	Morin et al. 2015
GU187215.1	Antarctica_B	Morin et al. 2010	KR180355.1	Antarctica_B	Morin et al. 2015
GU187216.1	Atlantic (Gulf of Mexico)	Morin et al. 2010	KR180356.1	Antarctica_A	Morin et al. 2015
GU187217.1	Antarctica_A	Morin et al. 2010	KR180357.1	Antarctica_A	Morin et al. 2015
GU187218.1	Antarctica_A	Morin et al. 2010	KR180358.1	Resident	Morin et al. 2015
GU187219.1	Antarctica_A	Morin et al. 2010	KR180359.1	ETP	Morin et al. 2015
HQ405752.3	Atlantic	Foote et al. 2011	KR180360.1	Crozet	Morin et al. 2015
KF164610.1	Unknown	Foote et al. 2013a	KR180361.1	Offshore	Morin et al. 2015
KF418372.1	Unknown	Foote et al. 2013b	KR180362.1	ETP	Morin et al. 2015
KF418373.1	Atlantic	Foote et al. 2013b	KR180363.1	ETP	Morin et al. 2015
KF418374.1	Atlantic	Foote et al. 2013b	KR180364.1	Unknown	Morin et al. 2015
KF418376.1	Unknown	Foote et al. 2013b	KR180365.1	ETP	Morin et al. 2015
KF418379.1	Unknown	Foote et al. 2013b	KR180366.1	ETP	Morin et al. 2015
KF418380.1	Atlantic	Foote et al. 2013b	KR180367.1	ETP	Morin et al. 2015
KF418381.1	Atlantic	Foote et al. 2013b	MH062792.1	Transient	Filatova et al. 2018
KF418382.1	Atlantic	Foote et al. 2013b	NC_023889.1	Unknown	Morin et al. 2010

Table S4: Haplotype network killer whale duplicates

Table S 4: Duplicates of killer whale samples identified by PopART during haplotype network building.

Sample ID/accession number	Duplicates	Sample ID/accession number	Duplicates
GU187207.1	GU187207.1	GU187186.1	GU187186.1
	GU187209.1		Oorca16001
GU187210.1	GU187210.1		Oorca16004
	GU187211.2		Oorca16007
GU187213.1	GU187213.1		Oorca16011
	GU187215.1		Oorca16014
KF418386.1	KF418386.1		Oorca16019
	KF418387.1		Oorca16020
KR180339.1	KR180339.1		Oorca16022
	KR180354.1		Oorca16026
KF418373.1	KF418373.1		Oorca16027
	Oorca16070		Oorca16028
Oorca16016	Oorca16016		Oorca16031
	Oorca16056		Oorca16032
	Oorca16109		Oorca16034
	Oorca16125		Oorca16040
	Oorca16134		Oorca16041
	Oorca18019		Oorca16042
Oorca16008	Oorca16008		Oorca16044
	Oorca16021		Oorca16045
	Oorca16024		Oorca16046
	Oorca16030		Oorca16047
	Oorca16035		Oorca16049
	Oorca16036		Oorca16052
	Oorca16048		Oorca16069
	Oorca16073		Oorca16072
	Oorca16085		Oorca16082
	Oorca16090		Oorca16084
	Oorca16096		Oorca16087
	Oorca16102		Oorca16088
	Oorca16106		Oorca16094
	Oorca16111		Oorca16095
	Oorca16112		Oorca16103
	Oorca16113		Oorca16104
	Oorca16115		Oorca16105

	Oorca16116		Oorca16107
	Oorca16118		Oorca16108
	Oorca16120		Oorca16114
	Oorca16124		Oorca16117
	Oorca16126		Oorca16119
	Oorca16127		Oorca16121
	Oorca16128		Oorca16122
	Oorca16131		Oorca16123
	Oorca16132		Oorca16129
	Oorca16133		Oorca16130
	Oorca16137		Oorca17001
	Oorca16138		Oorca17027
	Oorca16139		Oorca17028
	Oorca17002		Oorca17030
	Oorca18003		Oorca17031
	Oorca18006		Oorca18001
	Oorca18007		Oorca18002
	Oorca18008		Oorca18009
	Oorca18010		Oorca18020
	Oorca18011		Oorca18024
	Oorca18012		Oorca18025
	Oorca18013		Oorca18026
	Oorca18014		Oorca18027
	Oorca18015	KF418372.1	KF418372.1
	Oorca18016		KF418376.1
	Oorca18017		KF418379.1
	Oorca18018		KF418391.1
	Oorca18021	GU187178.1	GU187178.1
	Oorca18022		NC_023889.1
	Oorca18023	GU187193.1	GU187193.1
	Oorca18028		GU187196.1
	Oorca18029	GU187198.1	GU187198.1
	Oorca18030		KR180307.1
KF418393.1	KF418393.1	Oorca16075	Oorca16075
	Oorca16057		Oorca16079
	Oorca16061	GU187171.1	GU187171.1
	Oorca16062		KR180352.1
	Oorca16063	GU187172.1	GU187172.1
	Oorca16064		GU187173.1

	Oorca16066		GU187174.1
	Oorca16067		KR180300.1
	Oorca16068		KR180303.1
	Oorca16074		KR180347.1
GU187202.1	GU187202.1	GU187160.1	GU187160.1
	KR180327.1		MH062792.1
Oorca16053	Oorca16053	GU187182.1	GU187182.1
	Oorca16065		GU187183.1
			Oorca16110

Table S5: Humpback whale sampling information

Table S 5: Humpback whale sample information on date and location of sampling. Samples in red were not used in the phylogenetic analysis.

Sample ID	Date	Location	Sample ID	Date	Location
Mnova16001	13/01/2016		Mnova18020	08/09/2018	Barents Sea
Mnova16002	13/01/2016		Mnova18021	08/09/2018	Barents Sea
Mnova16003	01/02/2016	Vengsøyfjorden	Mnova18022	09/09/2018	Barents Sea
Mnova16004	01/02/2016	Vengsøysundet	Mnova18023	09/09/2018	Barents Sea
Mnova16005	01/02/2016	Vengsøyfjorden	Mnova18024	09/09/2018	Barents Sea
Mnova16006	01/02/2016	Vengsøysundet	Mnova18025	09/09/2018	Barents Sea
Mnova16007	01/02/2016	Vengsøyfjorden	Mnova18026	09/09/2018	Barents Sea
Mnova16008	01/02/2016	Vengsøysundet	Mnova18027	09/09/2018	Barents Sea
Mnova16009	06/02/2016	Sessøyfjord	Mnova18028	09/09/2018	Barents Sea
Mnova16010	06/02/2016	Sessøyfjord	Mnova18029	09/09/2018	Barents Sea
Mnova16011	06/02/2016	Sessøyfjord	Mnova18030	09/09/2018	Barents Sea
Mnova16012	06/02/2016	Sessøyfjord	Mnova18031	09/09/2018	Barents Sea
Mnova16013	06/02/2016	Sessøyfjord	Mnova18032	11/09/2018	Barents Sea
Mnova16014	06/02/2016	Sessøyfjord	Mnova18033	08/01/2019	Skjervøy
Mnova16015	20/02/2016	Ersfjord	Mnova18034	08/01/2019	Skjervøy
Mnova16016	20/02/2016	Ersfjord	Mnova18035	08/01/2019	Skjervøy
Mnova16017	20/02/2016	Ersfjord	Mnova18036	09/01/2019	Skjervøy
Mnova16018	28/01/2016	Gryllefjord, Danger reefs	Mnova18037	09/01/2019	Skjervøy
Mnova16019	28/01/2016	Gryllefjord, Teistneset	Mnova18038	09/01/2019	Skjervøy
Mnova16020	28/01/2016	Gryllefjord, Teistneset	Mnova18039	09/01/2019	Skjervøy
Mnova16021	28/01/2016	Gryllefjord, Teistneset	Mnova18040	19/01/2019	Skjervøy
Mnova16022	28/01/2016	Gryllefjord	Mnova18041	19/01/2019	Skjervøy
Mnova16023	28/01/2016	Gryllefjord, Teistneset	Mnova18042	20/01/2019	Skjervøy

Mnova16024	22/11/2016		Mnova18043	20/01/2019	Skjervøy
Mnova16025	31/12/2016	Skulsfjord	Mnova18044	20/01/2019	Skjervøy
Mnova16026	14/12/2016	Fiskøya	Mnova18045	19/01/2019	Skervøy
Mnova16027	13/12/2016	Skulsfjord	Mnova18046	23/01/2019	Skervøy
Mnova16028	07/11/2016	Sandoya	Mnova18047	23/01/2019	Skervøy
Mnova16029	07/11/2016	Sandoya	Mnova18048	24/01/2019	Skervøy
Mnova17001	14/11/2017	Skjervoy	Mnova18049	24/01/2019	Skervøy
Mnova17002	14/11/2017	Skjervoy	Mnova18050	24/01/2019	Skervøy
Mnova17003	14/11/2017	Skjervoy	Mnova18051	24/01/2019	Skervøy
Mnova17004	14/11/2017	Skjervoy	Mnova18052	26/10/2018	Skjervøy
Mnova17005	14/11/2017	Skjervoy	Mnova18053	26/10/2018	Skjervøy
Mnova17006	14/11/2017	Skjervoy	Mnova18054	27/10/2018	Skjervøy
Mnova17007	04/01/2017		Mnova18055	06/11/2018	Skjervøy
Mnova17008	04/01/2017		Mnova18056	06/11/2018	Skjervøy
Mnova17009	13/11/2017	Grotfjord	Mnova18057	06/11/2018	Skjervøy
Mnova17010	15/01/2017		Mnova18058	06/11/2018	Skjervøy
Mnova17011	13/01/2017	Grotfjord	Mnova18059	06/11/2018	Skjervøy
Mnova17012	13/01/2017	Grotfjord	Mnova18060	06/11/2018	Skjervøy
Mnova17013	13/01/2017	Grotfjord	Mnova18061	06/11/2018	Skjervøy
Mnova17014	12/01/2017	Ersfjorden	Mnova18062	07/11/2018	Skjervøy
Mnova17015	11/01/2017	Ersfjorden	Mnova18063	07/11/2018	Skjervøy
Mnova18001	13/11/2018	Skjervøy	Mnova18064	07/11/2018	Skjervøy
Mnova18002	04/09/2018	Barents Sea	Mnova18065	07/11/2018	Skjervøy
Mnova18003	04/09/2018	Barents Sea	Mnova18066	07/11/2018	Skjervøy
Mnova18004	04/09/2018	Barents Sea	Mnova18067	07/11/2018	Skjervøy
Mnova18005	04/09/2018	Barents Sea	Mnova18068	13/11/2018	Skjervøy
Mnova18006	04/09/2018	Barents Sea	Mnova18069	13/11/2018	Skjervøy
Mnova18007	05/09/2018	Barents Sea	Mnova18070	15/11/2018	Skjervøy
Mnova18008	05/09/2018	Barents Sea	Mnova18071	16/11/2018	Skjervøy
Mnova18009	07/09/2018	Barents Sea	Mnova18072	02/12/2018	Skjervøy
Mnova18010	07/09/2018	Barents Sea	Mnova18073	02/12/2018	Skjervøy
Mnova18011	07/09/2018	Barents Sea	Mnova18074	03/12/2018	Skjervøy
Mnova18012	07/09/2018	Barents Sea	Mnova18075	03/12/2018	Skjervøy
Mnova18013	07/09/2018	Barents Sea	Mnova18076	04/12/2018	Skjervøy
Mnova18014	07/09/2018	Barents Sea	Mnova18077	04/12/2018	Skjervøy
Mnova18015	07/09/2018	Barents Sea	Mnova18078	04/12/2018	Skjervøy
Mnova18016	07/09/2018	Barents Sea	Mnova18079	04/12/2018	Skjervøy
Mnova18017	07/09/2018	Barents Sea	Mnova18080	04/12/2018	Skjervøy
Mnova18018	08/09/2018	Barents Sea	Mnova18081	04/12/2018	Skjervøy

Mnova18019	08/09/2018	Barents Sea	Mnova18082	04/12/2018	Skjervøy

Table S6: Humpback whale haplotypes

Table S 6: Humpback whale samples divided into haplotypes identified in this study

Sample ID	Location	Haplotype	Sample ID	Location	Haplotype
Mnova16001	Unknown	Haplotype 1	Mnova16016	Ersfjord	Haplotype 2
Mnova16002	Unknown		Mnova16022	Gryllefjord	
Mnova16003	Vengsoy		Mnova16023	Gryllefjord	
Mnova16008	Vengsoy		Mnova16027	Skulsfjord	
Mnova16010	Sessoy		Mnova17008	Unknown	
Mnova16011	Sessoy		Mnova17015	Ersfjord	
Mnova16014	Sessoy		Mnova18008	Barents Sea	
Mnova16018	Gryllefjord		Mnova18010	Barents Sea	
Mnova16020	Gryllefjord		Mnova18021	Barents Sea	
Mnova16025	Skulsfjord		Mnova18022	Barents Sea	
Mnova17001	Skjervoy		Mnova18028	Barents Sea	
Mnova17004	Skjervoy		Mnova18029	Barents Sea	
Mnova17005	Skjervoy		Mnova18030	Barents Sea	
Mnova17006	Skjervoy		Mnova18037	Skjervoy	
Mnova17009	Grotfjord		Mnova18041	Skjervoy	
Mnova17010	Unknown		Mnova18042	Skjervoy	
Mnova17012	Grotfjord		Mnova18046	Skjervoy	
Mnova17014	Ersfjord		Mnova18054	Skjervoy	
Mnova18002	Barents Sea		Mnova18001	Skjervoy	Haplotype3
Mnova18005	Barents Sea		Mnova18016	Barents Sea	
Mnova18006	Barents Sea		Mnova18079	Skjervoy	
Mnova18007	Barents Sea		Mnova18081	Skjervoy	
Mnova18009	Barents Sea		Mnova18082	Skjervoy	
Mnova18011	Barents Sea		Mnova16021	Gryllefjord	Haplotype 4
Mnova18012	Barents Sea		Mnova17007	Unknown	
Mnova18014	Barents Sea		Mnova18066	Skjervoy	
Mnova18015	Barents Sea		Mnova18067	Skjervoy	
Mnova18017	Barents Sea		Mnova16006	Vengsoy	Haplotype 5
Mnova18020	Barents Sea		Mnova18004	Barents Sea	
Mnova18024	Barents Sea		Mnova18075	Skjervoy	
Mnova18026	Barents Sea		Mnova18018	Barents Sea	Haplotype 6
Mnova18031	Barents Sea		Mnova18068	Skjervoy	

Mnova18032	Barents Sea		Mnova18070	Skjervoy	
Mnova18034	Skjervoy		Mnova18047	Skjervoy	Haplotype 7
Mnova18035	Skjervoy		Mnova18004	Barents Sea	Haplotype 8
Mnova18036	Skjervoy		Mnova18027	Barents Sea	Haplotype 9
Mnova18039	Skjervoy		Mnova18023	Barents Sea	Haplotype 10
Mnova18040	Skjervoy		Mnova16015	Ersfjord	Haplotype 11
Mnova18043	Skjervoy		Mnova17002	Skjervoy	Haplotype 12
Mnova18049	Skjervoy		Mnova16019	Gryllefjord	Haplotype 13
Mnova18051	Skjervoy		Mnova18025	Barents Sea	Haplotype 14
Mnova18052	Skjervoy		Mnova18013	Barents Sea	Haplotype 15
Mnova18053	Skjervoy		Mnova16026	Fiskoy	Haplotype 16
Mnova18061	Skjervoy		Mnova18065	Skjervoy	Haplotype 17
Mnova18071	Skjervoy		Mnova18045	Skjervoy	Haplotype 18
Mnova18074	Skjervoy				
Mnova18076	Skjervoy				
Mnova18077	Skjervoy				
Mnova18078	Skjervoy				

Table S7: GenBank humpback whale sequences

Table S 7: Humpback whale full mitogenomes downloaded from GenBank.

Accession number	Location	Source
MF409246.1	Iceland	Arnason et al. 2018
AP006467.1	Antarctica	Sasaki et al. 2005
NC_006927.1	Unknown	Sasaki et al. 2005

Table S8: GenBank humpback whale CR sequences for haplotype networks

Table S 8: Mitogenome CR sequences and location information used for haplotype network building

Accession number	Location	Source
AF419263.1	Eastern Australia	Valsecchi et al. 2002
AF419264.1	Eastern Australia	Valsecchi et al. 2002
AF419266.1	Eastern Australia	Valsecchi et al. 2002
AF419270.1	Eastern Australia	Valsecchi et al. 2002
AY329845.2	Brazil	Engel et al. 2008
AY329854.2	Brazil	Engel et al. 2008
AY329856.2	Brazil	Engel et al. 2008

AY329862.2	Brazil	Engel et al. 2008
AY329865.2	Brazil	Engel et al. 2008
AY329873.2	Brazil	Engel et al. 2008
AY329881.2	Brazil	Engel et al. 2008
AY329885.2	Brazil	Engel et al. 2008
AY329886.2	Brazil	Engel et al. 2008
AY329889.2	Brazil	Engel et al. 2008
AY329891.2	Brazil	Engel et al. 2008
AY329893.2	Brazil	Engel et al. 2008
AY329898.2	Brazil	Engel et al. 2008
AY329899.2	Brazil	Engel et al. 2008
AY329906.2	Brazil	Engel et al. 2008
AY329910.2	Brazil	Engel et al. 2008
AY329911.2	Brazil	Engel et al. 2008
AY329914.2	Brazil	Engel et al. 2008
AY329920.2	Brazil	Engel et al. 2008
AY329923.2	Brazil	Engel et al. 2008
AY329925.2	Brazil	Engel et al. 2008
AY329926.2	Antarctica area II	Engel et al. 2008
AY329927.2	Brazil	Engel et al. 2008
AY329935.2	Brazil	Engel et al. 2008
AY329939.2	Brazil	Engel et al. 2008
AY329942.2	Brazil	Engel et al. 2008
AY329948.2	Brazil	Engel et al. 2008
AY329959.2	Brazil	Engel et al. 2008
AY329960.2	Brazil	Engel et al. 2008
AY329961.2	Brazil	Engel et al. 2008
AY329962.2	Brazil	Engel et al. 2008
AY329963.2	Brazil	Engel et al. 2008
AY329964.2	Brazil	Engel et al. 2008
AY329974.2	Brazil	Engel et al. 2008
AY329983.2	Brazil	Engel et al. 2008
AY329984.1	Brazil	Engel et al. 2008
AY329993.2	Brazil	Engel et al. 2008
AY330062.2	Antarctica area I	Engel et al. 2008
AY330092.2	Antarctica area I	Engel et al. 2008
AY330094.2	Antarctica area I	Engel et al. 2008
AY791295.1	Alaska, USA	Witteveen et al. 2004
AY791296.1	Alaska, USA	Witteveen et al. 2004

AY791323.1	Alaska, USA	Witteveen et al. 2004
AY791325.1	Alaska, USA	Witteveen et al. 2004
AY791341.1	Alaska, USA	Witteveen et al. 2004
AY791348.1	Alaska, USA	Witteveen et al. 2004
GQ872085.1	Western South Pacific	Valsecchi et al. 2002
GQ872086.1	Western South Pacific	Valsecchi et al. 2002
GQ872090.1	Western South Pacific	Valsecchi et al. 2002
GQ872091.1	Western South Pacific	Valsecchi et al. 2002
GQ872096.1	Western South Pacific	Valsecchi et al. 2002
GQ872098.1	Western South Pacific	Valsecchi et al. 2002
GQ872099.1	Western South Pacific	Valsecchi et al. 2002
GQ872101.1	Western South Pacific	Valsecchi et al. 2002
GQ872104.1	Western South Pacific	Valsecchi et al. 2002
GQ872110.1	Western South Pacific	Valsecchi et al. 2002
KU685434.1	Southern Ocean	Amaral et al. 2016
KU685436.1	Southern Ocean	Amaral et al. 2016
KU685443.1	Southern Ocean	Amaral et al. 2016
KU685451.1	Southern Ocean	Amaral et al. 2016
KU685453.1	Southern Ocean	Amaral et al. 2016
KU685457.1	Southern Ocean	Amaral et al. 2016
KU685465.1	Southern Ocean	Amaral et al. 2016
KU685468.1	Southern Ocean	Amaral et al. 2016

Table S9: GenBank humpback whale CR sequences for phylogenetic tree

Table S 9: Mitogenome CR sequences used in the global phylogenetic tree. Numbers in parenthesis after the accession number represent the amount of duplicates of the haplotype.

Accession number	Source	Accession number	Source
AF068067.1 (6)	Baker et al. 1993	AY329925.2 (3)	Engel et al. 2008
AF068068.1	Baker et al. 1993	AY329926.2 (4)	Engel et al. 2008
AF068069.1 (32)	Baker et al. 1993	AY329927.2 (3)	Engel et al. 2008
AF068070.1	Baker et al. 1993	AY329935.2 (3)	Engel et al. 2008
AF068071.1 (10)	Baker et al. 1993	AY329939.2 (2)	Engel et al. 2008
AF068072.1 (4)	Baker et al. 1993	AY329942.2 (12)	Engel et al. 2008
AF068075.1	Baker et al. 1993	AY329948.2 (6)	Engel et al. 2008
AF068076.1 (26)	Baker et al. 1993	AY329959.2 (5)	Engel et al. 2008
AF068077.1 (2)	Baker et al. 1993	AY329960.2	Engel et al. 2008
AF068078.1 (8)	Baker et al. 1993	AY329961.2	Engel et al. 2008

AF068079.1 (9)	Baker et al. 1993	AY329962.2	Engel et al. 2008
AF068080.1 (5)	Baker et al. 1993	AY329963.2	Engel et al. 2008
AF068083.1	Baker et al. 1993	AY329964.2	Engel et al. 2008
AF068084.1	Baker et al. 1993	AY329974.2 (4)	Engel et al. 2008
AF068085.1 (2)	Baker et al. 1993	AY329983.2 (4)	Engel et al. 2008
AF068086.1	Baker et al. 1993	AY329984.1	Engel et al. 2008
AF068087.1	Baker et al. 1993	AY329993.2 (2)	Engel et al. 2008
AF068088.1 (7)	Baker et al. 1993	AY330062.2	Engel et al. 2008
AF068089.1 (6)	Baker et al. 1993	AY330092.2	Engel et al. 2008
AF068090.1 (4)	Baker et al. 1993	AY330094.2	Engel et al. 2008
AF068091.1	Baker et al. 1993	AY340954.1-Fin-whale	McEwing, unpublished
AF068092.1 (18)	Baker et al. 1993	AY340955.1-fin-whale	McEwing, unpublished
AF068093.1	Baker et al. 1993	AY340956.1-fin-whale	McEwing, unpublished
AF068094.1 (5)	Baker et al. 1993	AY791295.1 (16)	Witteveen et al. 2004
AF068095.1 (13)	Baker et al. 1993	AY791296.1 (24)	Witteveen et al. 2004
AF068097.1	Baker et al. 1993	AY791323.1	Witteveen et al. 2004
AF068098.1 (24)	Baker et al. 1993	AY791325.1	Witteveen et al. 2004
AF068099.1 (2)	Baker et al. 1993	AY791341.1	Witteveen et al. 2004
AF068101.1 (8)	Baker et al. 1993	AY791348.1	Witteveen et al. 2004
AF068102.1 (9)	Baker et al. 1993	AY822110.1 (5)	Valsecchi et al. 2002
AF068104.1 (10)	Baker et al. 1993	GQ872085.1	Valsecchi et al. 2002
AF068105.1	Baker et al. 1993	GQ872086.1	Valsecchi et al. 2002
AF068106.1 (10)	Baker et al. 1993	GQ872090.1	Valsecchi et al. 2002
AF068107.1 (12)	Baker et al. 1993	GQ872091.1	Valsecchi et al. 2002
AF068109.1 (6)	Baker et al. 1993	GQ872096.1	Valsecchi et al. 2002
AF068112.1 (4)	Baker et al. 1993	GQ872098.1	Valsecchi et al. 2002
AF068113.1	Baker et al. 1993	GQ872099.1 (2)	Valsecchi et al. 2002
AF068114.1 (3)	Baker et al. 1993	GQ872101.1 (2)	Valsecchi et al. 2002
AF419263.1 (2)	Valsecchi et al. 2002	GQ872104.1	Valsecchi et al. 2002
AF419264.1 (3)	Valsecchi et al. 2002	GQ872110.1	Valsecchi et al. 2002
AF419266.1	Valsecchi et al. 2002	GU942470.1 (4)	Palsbøll et al. 1995
AF419270.1 (2)	Valsecchi et al. 2002	GU942472.1 (5)	Palsbøll et al. 1995
AY329845.2 (9)	Engel et al. 2008	KU685434.1	Amaral et al. 2016
AY329854.2 (3)	Engel et al. 2008	KU685436.1	Amaral et al. 2016
AY329856.2 (3)	Engel et al. 2008	KU685443.1	Amaral et al. 2016
AY329862.2 (2)	Engel et al. 2008	KU685451.1	Amaral et al. 2016
AY329865.2 (6)	Engel et al. 2008	KU685453.1	Amaral et al. 2016
AY329873.2	Engel et al. 2008	KU685457.1	Amaral et al. 2016
AY329881.2	Engel et al. 2008	KU685465.1	Amaral et al. 2016

AY329885.2 (7)	Engel et al. 2008	KU685468.1	Amaral et al. 2016
AY329886.2	Engel et al. 2008	U76968.1 (2)	Palsbøll et al. 1995
AY329889.2 (5)	Engel et al. 2008	U76970.1	Palsbøll et al. 1995
AY329891.2 (2)	Engel et al. 2008	U76971.1	Palsbøll et al. 1995
AY329893.2 (6)	Engel et al. 2008	U76974.1	Palsbøll et al. 1995
AY329898.2 (3)	Engel et al. 2008	U76975.1	Palsbøll et al. 1995
AY329899.2	Engel et al. 2008	U76976.1	Palsbøll et al. 1995
AY329906.2	Engel et al. 2008	U76979.1	Palsbøll et al. 1995
AY329910.2 (5)	Engel et al. 2008	U76980.1	Palsbøll et al. 1995
AY329911.2 (2)	Engel et al. 2008	U76984.1	Palsbøll et al. 1995
AY329914.2	Engel et al. 2008	U76985.1	Palsbøll et al. 1995
AY329920.2 (3)	Engel et al. 2008	U76986.1	Palsbøll et al. 1995
AY329923.2 (2)	Engel et al. 2008	U76989.1	Palsbøll et al. 1995
		U76991.1	Palsbøll et al. 1995

Table S10: Haplotype network humpback whale duplicates

Table S 10: Duplicates of humpback whale samples identified by PopART during haplotype network building.

Sample ID/accession number	Duplicates	Sample ID/accession number	Duplicates
MF409246.1	MF409246.1	AP006467.1	AP006467.1
	Mnova16001		NC_006927.1
	Mnova16002	Mnova16021	Mnova16021
	Mnova16003		Mnova17007
	Mnova16008		Mnova18066
	Mnova16010		Mnova18067
	Mnova16011	Mnova16006	Mnova16006
	Mnova16014		Mnova18027
	Mnova16018		Mnova18044
	Mnova16020		Mnova18075
	Mnova16025	Mnova16016	Mnova16016
	Mnova17001		Mnova16022
	Mnova17004		Mnova16023
	Mnova17005		Mnova16027
	Mnova17006		Mnova17008
	Mnova17009		Mnova17015
	Mnova17010		Mnova18008
	Mnova17012		Mnova18010

	Mnova17014		Mnova18021
	Mnova18002		Mnova18022
	Mnova18005		Mnova18028
	Mnova18006		Mnova18029
	Mnova18007		Mnova18030
	Mnova18009		Mnova18037
	Mnova18011		Mnova18041
	Mnova18012		Mnova18042
	Mnova18014		Mnova18046
	Mnova18015		Mnova18054
	Mnova18017	Mnova18018	Mnova18018
	Mnova18020		Mnova18068
	Mnova18024		Mnova18070
	Mnova18026	Mnova18004	Mnova18004
	Mnova18031		Mnova18047
	Mnova18032	Mnova18001	Mnova18001
	Mnova18034		Mnova18016
	Mnova18035		Mnova18079
	Mnova18036		Mnova18081
	Mnova18039		Mnova18082
	Mnova18040		
	Mnova18043		
	Mnova18049		
	Mnova18051		
	Mnova18052		
	Mnova18053		
	Mnova18061		
	Mnova18071		
	Mnova18074		
	Mnova18076		
	Mnova18077		
	Mnova18078