Chapter

Phylogeny and Population Genetic Structure of Minke Whales Worldwide: A Review of Recent Studies

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Abstract

In 1998, two species of minke whales were recognized based on the review of the morphological and genetic information available at that time: the Antarctic minke whale (*Balaenoptera bonaerensis*), which is restricted to the Southern Hemisphere, and the cosmopolitan common minke whale (*Balaenoptera acutorostrata*). Furthermore, three sub-species of the common minke whale were recognized: the North Atlantic (*B. a. acutorostrata*), North Pacific (*B. a. scammoni*) and Southern Hemisphere (*B. a. subsp*.). This chapter reviews the genetic studies on minke whales conducted after 1998. The review is organized by topic, e.g., those studies focused on phylogeny and other matters most relevant for taxonomy, and those focused on population genetic structure within oceanic basins most relevant for conservation and management. On the former topic, the new genetic information, whilst strongly supporting the minke whale taxonomic classification recognized in 1998, also reveals substantial genetic differentiation within the Southern Hemisphere common minke whales, with subsequent taxonomic implications. On the latter topic, results from different analytical procedures have provided information on population identification and structure in the Indo-Pacific sector of the Antarctic and western North Pacific, but they have failed to identify unequivocally any population within the North Atlantic common minke whales.

Keywords: Antarctic minke whale, North Pacific common minke whale, North Atlantic common minke whale, Southern Hemisphere common minke whale, dwarf minke whale, genetics, taxonomy, population structure

1. Introduction

Minke whales are members of the Order Cetacea. They are the smallest species within the suborder Mysticeti (baleen whales), usually not exceeding the 10 m in body length. They are characterized by a sharply pointed head that looks V-shaped when see from above, and they present a sharp longitudinal ridge that runs along the

top of the rostrum [1]. Minke whales are the most abundant of the baleen whales and they are hunted in limited numbers by some countries for commercial (Japan and Norway) or aboriginal subsistence (Greenland) purposes.

Until relatively recently, only one species of minke whale was thought to exist: *Balaenoptera acutorostrata*. This even though historical morphological [2–6] and genetics [7–9] data collected from extant populations pointed out to substantial differentiation within the minke whales.

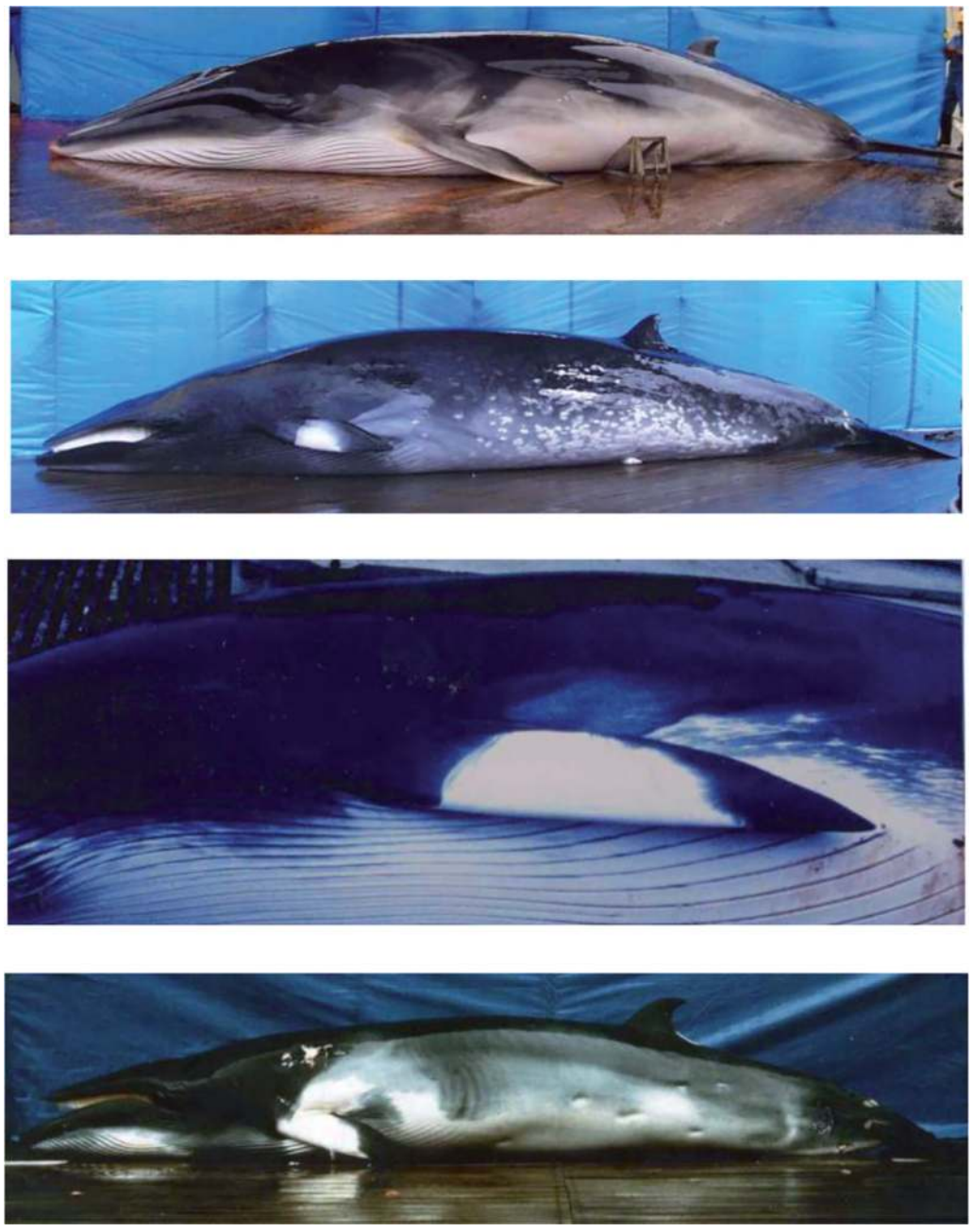

Figure 1.
External morphology of minke whales. From top to bottom: Antarctic minke whale, North Pacific common minke whale, North Atlantic common minke whale and Southern Hemisphere common minke whale (dwarf minke whale).

In 1998, based on a review of both morphological and genetic data, two species of minke whales were recognized, the Antarctic minke whale (*Balaenoptera bonaerensis*), which is restricted to the Southern Hemisphere, and the cosmopolitan common minke whale (*B. acutorostrata*) [10]. Furthermore, three sub-species of the common minke whale were recognized, North Atlantic (*B. a. acutorostrata*), North Pacific (*B. a. scammoni*) and Southern Hemisphere (*B. a. subsp*.) [10]. The common minke whale in the Southern Hemisphere is commonly referred to as the 'dwarf' minke whale [6]. **Figure 1** shows the external morphology of minke whale species and sub-species. As seen in **Figure 1**, the main external morphological character that most readily distinguished the two species is a white flipper patch that is only present in the common minke whale.

Several genetic studies of minke whales have been conducted since the 1998 review. Some studies have focused on phylogenetic issues while others have focused on elucidating population genetic structure in each oceanic basin. This chapter aims to provide a short review of recent genetic studies, outlining the main new findings and implications. After introducing the genetic markers in Section 2, in Section 3, we review the studies that focus primarily on phylogeny and other matters that are relevant to taxonomy and then, in Section 4, we concentrate on the studies on the population genetic structure of each species and sub-species by oceanic basin (Southern Hemisphere, North Atlantic and North Pacific).

Both information on taxonomy and population identification and structure of minke whales are important and necessary for effective decision-making about conservation and sustainable use of the species.

2. Genetic markers

Two main genetic markers have been used in recent genetic analyses of minke whales, mitochondrial DNA (mtDNA) control region sequences and microsatellite DNA (msDNA, a nuclear marker) genotypes, which are briefly explained here based on [11].

The mitochondrial genome is a circular, double-stranded molecule ranging in size from 16,500 to 17,600 base-pairs (bp) in cetaceans. The main features of mtDNA are (a) maternal inheritance, (b) no recombination during reproduction and (c) it is haploid. Features (a) and (c) mean that the effective population size for the mtDNA genome is ¼ of that for nuclear markers. Sequence changes in animal mitochondrial genomes are of four types: sequence arrangements; additions; deletions; and nucleotide substitutions. The substitution rate is not constant across the mitochondrial genome. The most variable part is where replication begins (the 'control region'). The control region is the only major non-coding region in the mitochondrial genome. In whales, its length is approximately 1000 bp. In most studies on minke whales, the sequence of the first 300-500 bp in the control region is determined, which is the most variable part.

MsDNA or simple tandem repeats (STRs) are segments of non-coding nuclear DNA containing a varying number (different alleles) of tandem repeats of short sequences of less than six nucleotides. As a nuclear marker, they are diploid with recombination during reproduction. They are abundant and widely distributed throughout the mammalian genome. MsDNA is highly variable, presenting a large number of alleles at each locus, selectively neutral, inherited in standard Mendelian fashion and allelically codominant. MsDNA generally evolves by changes in the number of repeats, i.e., in the length of the repetitive region. MsDNA alleles can be distinguished by differences in the length of the repetitive region. They predominantly

mutate by insertion or deletion of repeats. In most studies on minke whales, a set of approximately 12–16 msDNA loci are used.

Most of the recent genetic studies on minke whales have made combined use of these two genetic markers, which presents several advantages. Some of the genetic criteria for taxonomic definition require results of both markers (see below). Different species of large whales can produce hybrid whales and such cases can be detected by the combined use of mtDNA and msDNA. In studies on population identification and structure, parallel analyses of Mendelian and maternally inherited loci are particularly important. Some species may display maternally directed phylopatry. In such cases, genetic differences can be found for the mtDNA but not for msDNA. The use of msDNA in addition to mtDNA allows for an investigation of kinship, which is important information for the interpretation of population structure.

Details of laboratory procedures for mtDNA and msDNA in minke whales can be found in [12].

3. Phylogenetic and other studies relevant for taxonomy

Several genetic studies addressing phylogenetic and other aspects relevant for taxonomy were conducted after the 1998 review in [10]. All those studies used samples from minke whale worldwide [13–18]. Oceanic basins covered by the genetic sampling in recent studies are shown in **Figure 2**.

A brief description and main findings of these studies are presented below. Several phylogenetic inference methods were used to evaluate observed heritable traits, such as mtDNA sequences, under a specified model of the evolution of the traits. Taxonomic classification is now usually based on phylogenetic data. Details of the phylogenetic inference methods are not given here however relevant bibliographic references on the methods are provided for interested readers in the sections below.

3.1 Speciation and divergence time

The focus of the first post-1998 study involving minke whales was a case study to investigate the radiation and speciation of pelagic organisms during the period of global warming [13]. The study was based on mtDNA control region sequences (340 bp) in samples of Antarctic minke whales (n = 180), North Atlantic (n = 102) and North Pacific (n = 161) common minke whales and Southern Hemisphere common or dwarf minke whales (n = 23 from the western South Atlantic, WSA and western South Pacific, WSP). A total of 187 haplotypes (unique sequences) were determined. The genealogical relationship among a sub-set of 60 haplotypes was estimated using the NUCML program in the MOLPHY computer package [19], the BASEML program in the PAML computer package [20] and the TREE-PUZZLE program of the quartet-puzzling (QP) method [21]. Divergence time was estimated by applying a molecular clock model using a calibration point that minke whales and the gray whales (*Eschrichtius robustus*) separated 20 million years ago (Ma) [22].

The study provided evidence for phylogenetic differentiation not only between the two species of minke whales but also among North Atlantic, North Pacific and Southern Hemisphere common minke whales. The study estimated that the two species of minke whales diverged in the Southern Hemisphere less than 5 Ma, and that the current sub-species of the common minke whales diverged after the Pliocene some 1.5 Ma.

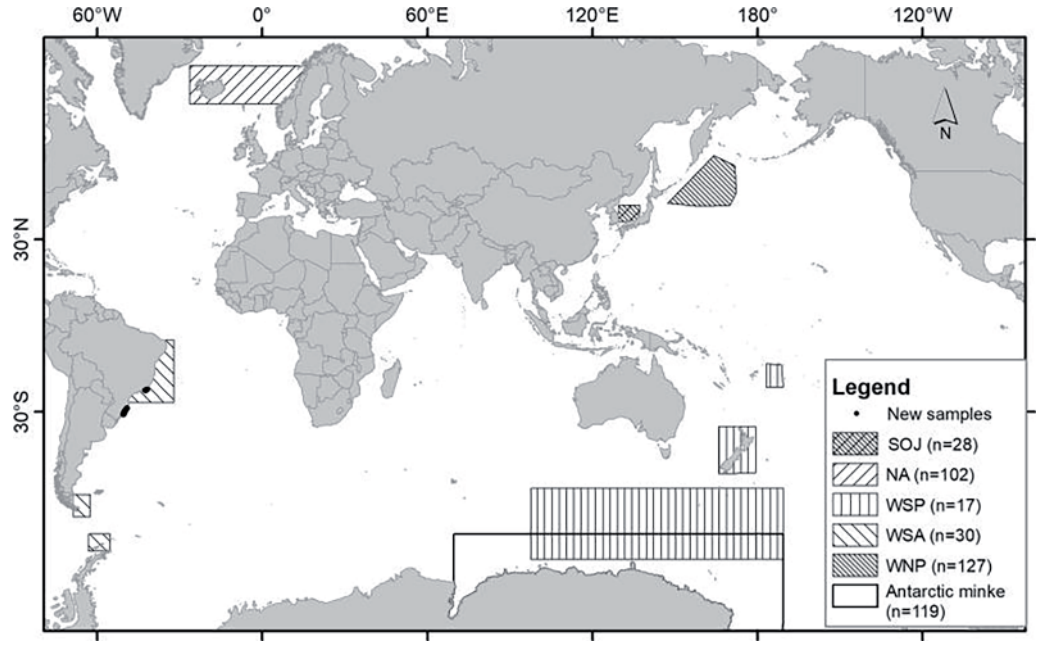

Figure 2.
Oceanic basins covered by the genetic sampling for the phylogenetic and other studies relevant for the taxonomy of minke whales. SOJ = Sea of Japan, NA = North Atlantic, WSP=Western South Pacific, WSA = Western South Atlantic, WNP=Western North Pacific, Antarctic minke whale = Antarctic Ocean (modified from [18]).

Based on their analysis, the authors hypothesized that prolonged periods of global warming facilitate speciation in pelagic marine species that depend on upwelling [13].

3.2 Phylogenetic analyses

Three relevant studies are described here [14, 16, 18]. The first study [14] used mtDNA control region sequences (327 bp) and a similar sample set of the previous study [13] but this time the study was focused to elucidate the population genetic structure of the Southern Hemisphere common minke whales using samples from WSA (n = 12) and WSP (n = 17) (**Figure 3**).

The genealogy of the mtDNA haplotypes was estimated using the neighbor-joining method (NJ) [23], minimum evolution (ME) [24], maximum likelihood (ML) [25] and maximum parsimony (MP) [26]. To evaluate the relative effects of divergence and migration between WSA and WSP whales, the approach in [27] modified for a finite mutation level [28] was used. Phylogenetic inferences derived from these methods were consistent, and similar to the inferences obtained in a previous study [13]. WSA common minke whale haplotypes (except one), clustered in a single clade, which nested within the North Atlantic common minke whale clade. On the other hand, WSP common minke whale haplotypes clustered in a different clade. The study showed that haplotypes from the WSA whales share more recent common ancestors with the North Atlantic minke whales than they do with the WSP minke whales. The analysis suggested a very low number of migrants by generation between WSA and WSP, which suggests that the WSA single haplotype in the WSP clade was unlikely to be a result of migration but rather due to incomplete lineage sorting [14].

The most recent genetic analysis on minke whales worldwide [18] was based on mtDNA control region sequences (313 bp) and msDNA (11 loci). The sample

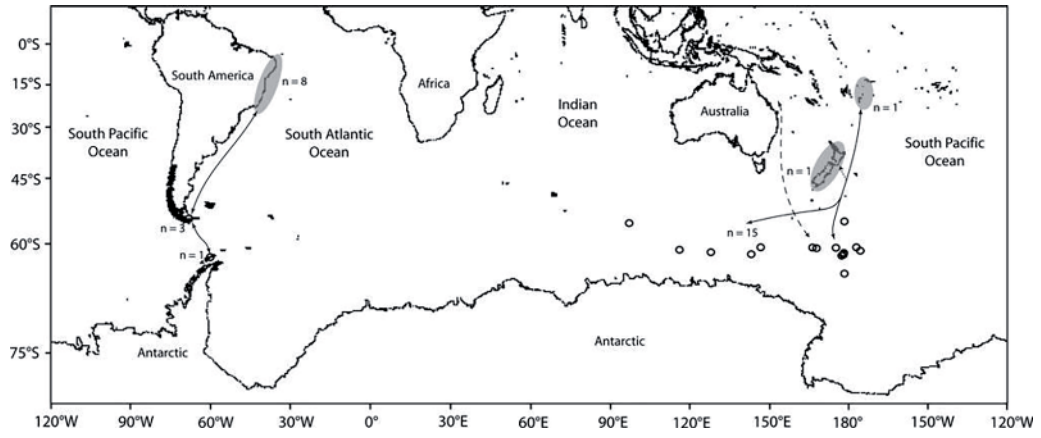

Figure 3.
The geographic position of Southern Hemisphere common minke whales (dwarf minke whales) samples used in [14]. Solid and dashed lines indicate possible migratory routes and possible connections, respectively (modified from [14]).

set for the mtDNA analysis was similar to those in the previous studies [13, 14] but the samples of the Southern Hemisphere common minke whales were increased (WSP, n = 17; WSA, n = 30), and msDNA was used in addition to mtDNA. A total of 148 haplotypes were determined. The genealogy of the mtDNA haplotypes was estimated using several methods including NJ, ML and Bayesian inferences (BI) [29]. The three methods provided similar results, and they were consistent with previous phylogenetic inferences [13, 14]. Results from the BI method are shown in **Figure 4**. This figure shows two main clades, one corresponding to Antarctic minke whales and the other to common minke whales. Furthermore, within the common minke whales clade, North Pacific, North Atlantic and Southern Hemisphere common minke whales clustered in different sub-clades.

Figure 4 shows that WSA and WSP common minke whales in the Southern Hemisphere clustered in different sub-clades (except the single WSA haplotype mentioned previously that clustered within the WSP sub-clade), and that the WSA haplotypes fell with the North Atlantic sub-clade.

This study estimated the net nucleotide substitutions (d_A) [30] between species and sub-species of minke whales. The d_A between the Antarctic and common minke whales was high (0.08 in average). The value among common minke whales from different oceanic basins averaged 0.026. The d_A between Southern Hemisphere WSP and WSA was 0.027 and that between the Sea of Japan and western North Pacific was 0.007 [18].

The msDNA analysis in [18] involved samples from three localities only (unfortunately, no samples from the North Atlantic common minke whales were considered): North Pacific and Southern Hemisphere (WSA and WSP) common minke whales. The pattern of msDNA differentiation was investigated by two indices, F_{ST} [31] and D_{SW} [32]. All pairwise comparisons among North Pacific, WSA and WSP yielded statistically significant differences and the values estimated between WSA and WSP were smaller than the values between each of these populations and North Pacific common minke whales. Therefore, North Pacific, Southern Hemisphere WSA and WSP not only were separated phylogenetically in their mtDNA but they differed significantly in their msDNA as well.

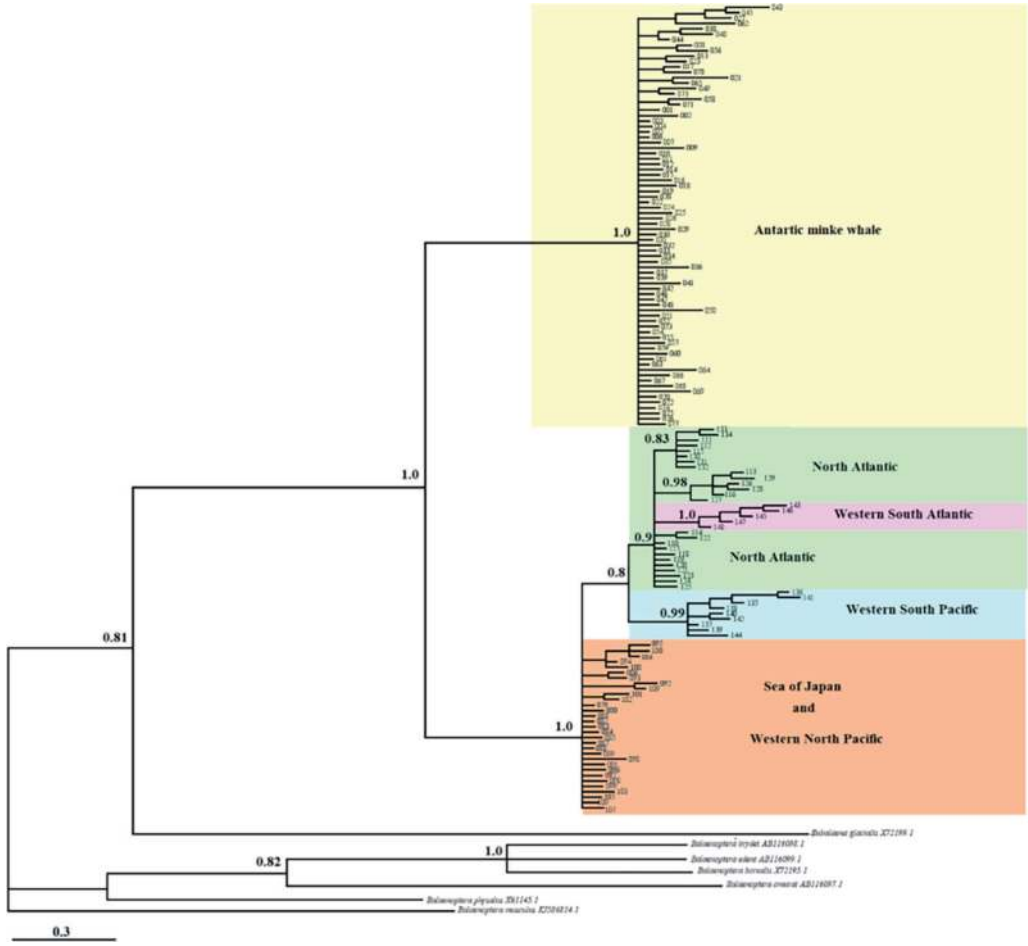

Figure 4.
Bayesian phylogenetic tree of minke whale mtDNA haplotypes. Values indicate support for each node according to the maximum posterior probabilities>80%. Scale bar represents substitutions per nucleotide site. NA = North Atlantic; WSA: Western South Atlantic; WSP = Western South Pacific; SOJ = Sea of Japan; WNP = Western North Pacific (modified from [18]).

Although, the third study was focused to investigate hybrids between the two species of minke whales [16], it also provided information on genetic differentiation between the Antarctic and common minke whales species as well among common minke whales from different oceanic basins. The study was based on mtDNA control region sequences (287 bp) and msDNA (11 loci), and samples from the Antarctic minke whale (n = 91), North Atlantic (n = 91), North Pacific (n = 95) and Southern Hemisphere (WSP) (n = 9) common minke whales. The genealogy of the mtDNA haplotype was estimated using the NJ method and the inferences obtained were similar to the other studies [13–14, 18]. The msDNA F_{ST} estimates were calculated and Bayesian cluster analysis was also performed using the program *STRUCTURE* [33]. Pairwise F_{ST} estimates revealed that the Antarctic minke whales, North Atlantic, North Pacific and Southern Hemisphere (WSP) common minke whales were genetically distinct from each other. The Bayesian cluster analysis supported the F_{ST} results, showing large genetic differences between the Antarctic and common minke whales as well among common minke whales from North Atlantic, North Pacific and Southern Hemisphere (WSP) [16].

3.3 Hybridization in minke whales

A genetic study based on both mtDNA (287 bp) control region sequences and msDNA (13 loci) reported the migration of an Antarctic minke whale into the Arctic Northeast Atlantic in 1996 [15]. The same study reported the occurrence of a hybrid whale in the North Atlantic in 2007. The analytical procedures for the identification of the hybrid involved the use of the Bayesian cluster analysis *STRUCTURE* and genetic assignment conducted in the program GeneClass2 [34]. The latter used a genetic baseline consisting of the three minke whale species and sub-species which had a large sample size (Southern Hemisphere common minke whales were excluded due to their small sample size), in addition to three sets of hybrids produced in the program HYBRIDLAB1.0 [35]. The 2007 hybrid was demonstrated to consist of a maternal contribution from an Antarctic minke whale and most likely paternal contribution from the North Atlantic common minke whale. Another case of a hybrid was identified using the same analytical procedures. It was a pregnant female captured in 2010 [16]. In this case, the genetic analyses by both markers confirmed that the mother was a hybrid displaying maternal and paternal contribution from North Atlantic common and Antarctic minke whales, respectively [16]. This study demonstrated for the first time, that hybrids between minke whale species may be fertile, and that they can back-cross.

3.4 Implications for taxonomy and suggestions for future works

Taxonomic definitions are associated with the term Evolutionary Significant Unit (ESU) [36, 37], defined in [37] as 'ESUs should be reciprocally monophyletic for mitochondrial DNA alleles and show significant divergence of allele frequencies at nuclear loci'. However, other authors have argued that the definition of ESUs should incorporate ecological data in addition to data on genetic variation of adaptive significance [38]. An example of ecological data could be discrete prey preferences of sympatric individuals. Other authors suggest the use of d_A values based on mtDNA: a review of analytical approaches for recognition of populations, sub-species and species based on mtDNA sequences suggested that species generally exhibit values of d_A greater than 0.02 and populations values less than 0.004 [39], and see also [18].

Considering these criteria, the post-1998 genetic results (with larger sample sizes and wider geographical range), strongly support the division of Antarctic and common minke whales as different species [10]. They clearly match the ESU definition (based on different phylogenetic inference methods), and the average estimated d_A between the Antarctic and common minke whales from different oceanic basins was estimated at 0.08.

Within the common minke whales, the North Pacific and Southern Hemisphere (WSP) match the ESU criterion. Their average d_A with common minke whales from other oceanic basins averaged 0.02 [18]. Then the status of sub-species is appropriated for North Pacific and Southern Hemisphere (WSP) common minke whales.

The case of the North Atlantic and Southern Hemisphere (WSA) common minke whales is more complex. This is because some of the mtDNA phylogenetic analyses showed haplotypes of common minke whales from WSA clustering within the North Atlantic common minke whale clade, therefore not matching the reciprocally monophyletic for mitochondrial DNA definition of ESU, although the status of sub-species is appropriate based on the d_A criterion. Therefore, while both Southern Hemisphere common minke whales (WSP and WSA) are clearly separated from North Pacific common minke whales matching all criteria for sub-species, the relationship between

WSA and North Atlantic common minke whales requires further investigation including additional genetic analyses based on larger samples from WSP and WSA using both mitochondrial and nuclear markers. In addition, genetic analyses of Southern Hemisphere common minke whales from other unstudied localities, e.g., the Western Indian Ocean [6], are required to elucidate further the phylogenetic relationship among Southern Hemisphere and North Atlantic common minke whales.

Finally, and following the criteria above, whales from the Sea of Japan and western North Pacific should be considered as populations of the North Pacific common minke whale.

The cases of hybridization between minke whale species and the study showing that such hybrids may be fertile, and that they can back-cross have some relevance to the taxonomy of minke whales. As noted in [16], it is not possible to resolve whether the observed migration of Antarctic minke whales to the Arctic, and hybridization between Antarctic minke whales and North Atlantic common minke whales are (a) random events that have occurred over a long period of time; (b) the result of a low number of Antarctic minke whales migrating from the Antarctic to the Arctic in the 1990s; or (c) represent a trend that is increasing in frequency. The authors in [16] further argued that the lack of hybrids in the large ($n > 15000$) Japanese genetic data sets infers that such events are not frequent. Unless the frequency of reproductive contact increases significantly in the future, the separation of the Antarctic minke whale and the North Atlantic common minke whale should not be challenged [16].

In summary, the recent genetic studies provide support for the classification recognized in the 1998 review [10] for two species, the Antarctic and the common minke whale, and at least three sub-species of the latter. Furthermore, these studies suggest a phylogenetic separation between Southern Hemisphere common minke whales from Western South Pacific and Western South Atlantic. Whales from these two localities differed significantly in mtDNA haplotype and msDNA allele frequencies. Phylogenetic analyses showed that haplotypes from the WSA whales share a more recent common ancestor with the North Atlantic common minke whales than they do with the WSP common minke whales.

4. Studies on population genetic structure in each oceanic basin

Minke whales were hunted commercially or under special permit in the Southern Hemisphere until the 2018/19 austral summer season, and they are hunted currently for limited numbers in the North Atlantic (commercial and aboriginal subsistence purposes), and western North Pacific (commercial purposes). Identification of populations within species and sub-species in each oceanic basin, therefore, is very important for conservation and management purposes. This is because different populations of the same species or subspecies may respond in different ways to levels of direct removals (e.g., catches, bycatches) and other types of environmental stress (e.g., habitat degradation) [18]. Population dynamics modeling is used to investigate the effect of different management strategies and environmental stressors at the population level. However, the identification of populations is not a trivial issue.

In each of the relevant oceanic basins, Southern Hemisphere, North Atlantic and North Pacific, minke whales are believed, like most baleen whale species, to undertake seasonal migrations between feeding grounds in higher latitudes in summer and breeding grounds in lower latitudes in the tropical or temperate regions in winter.

However, there are few direct observations of this linkage, and information of minke whale breeding grounds in low latitudes is poor. Ideally, genetic analyses on population identification should be carried out based on samples collected in breeding grounds. However, all genetic analyses on minke whale population identification have been based on samples collected in feeding grounds and migratory corridors, where different populations may mix spatially and/or temporally.

The International Whaling Commission (IWC) has defined areas for the management (i.e., the setting of catch limits) of minke whales in each oceanic basin based upon a variety of data types, genetic and non-genetic (e.g., see [40]) since the earliest days of management, often based upon limited information or analogy. Most recent studies have focused on the correspondence of the set management boundaries with the available genetic information and revising the boundaries as appropriate to ensure that overexploitation does not occur. The primary management tool used by the IWC Scientific Committee to provide advice on commercial whaling catch limits is known as the Revised Management Procedure or RMP that focusses on providing robust management advice in the light of inevitable scientific uncertainty (e.g., [41]). Uncertainty in stock structure is one of the most influential in terms of providing robust advice. The philosophy adopted under the RMP (and the sister approach for aboriginal subsistence whaling known as the AWMP or Aboriginal Subsistence Whaling Management Procedure) with respect to stock structure is that it is not often, if ever, possible to arrive at only one plausible stock structure hypothesis from the available data. Rather than in the past when the 'best' hypothesis (and boundaries) was determined and then fixed management boundaries for the 'unit-to-conserve' (usually a population) chosen, the RMP approach says that catch limits must be set that are robust to all plausible hypotheses and that these hypotheses should be regularly reviewed in the light of new data. Of course, deciding what comprises 'plausible' is a complex and difficult issue and one which has driven much of the work described below, especially for the North Pacific common minke whale.

In this section, the most recent genetic analyses on population identification and structure in minke whales are reviewed for each species and sub-species in each relevant oceanic basin.

The method most often used for the identification of populations within an oceanic basin was hypothesis testing under the null hypothesis of panmixia. Under this method, mtDNA haplotype and/or msDNA allele frequencies between two geographically grouped samples are compared using several statistical tests. More recently, spatially explicit clustering approaches, for example, sPCA, GENELAND, TESS and BAPS have been used to investigate population identification and structure.

Details of the statistical tests and clustering approaches are not given here however relevant references on the methods are provided for interested readers in the sections below.

4.1 Antarctic minke whales

The IWC's management areas for baleen whales (excluding the Bryde's whale *Balaenoptera edeni*) are shown in **Figure 5**. These management areas were used during the former commercial whaling of Antarctic minke whales but were based upon information from other baleen whales, notably blue (*B. musculus*), fin (*B. physalus*) and humpback (*Megaptera novaeangliae*) whale catch distributions and mark-recapture records. Most of the recent genetic studies have been focused in the Indian and Pacific sectors of the Antarctic (mainly Areas IV and V in **Figure 5**) where a large number of genetic samples were available from the Japanese Whale Research Program

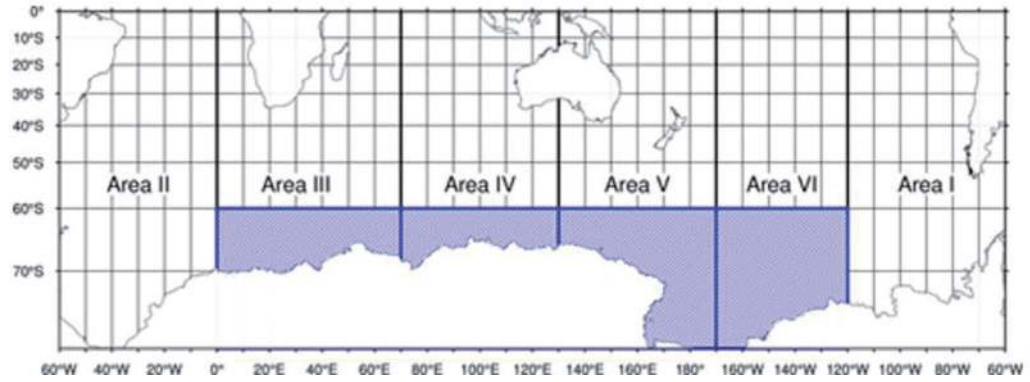

Figure 5.
Management areas defined by the International Whaling Commission for the management of baleen whales (except the Bryde's whale) in the Southern Hemisphere. These areas were used for the management of the Antarctic minke whale in the period of commercial whaling, which was stopped in the 1986/87 austral summer season. Most of the recent genetic studies on population structure have been conducted in the shaded area.

under Special Permit in the Antarctic, Phases I and II (JARPA and JARPAII). Surveys of these research programs were conducted systematically in the Indo Pacific sector of the Antarctic in summer from 1987/88 to 2014/15.

There are no genetic samples from Antarctic minke whales from low latitude regions of the eastern Indian Ocean and western South Pacific where breeding grounds of this species in this region are assumed to occur. The most recent genetic studies were based therefore on samples collected by the JARPA and JARPAII programs in the Antarctic feeding grounds of Areas III east, IV, V and VI west. Those studies were summarized in [42], and the most relevant aspects are highlighted here.

Previous morphometric, biological and genetic studies based on mtDNA and msDNA led to the conclusion that Antarctic minke whales in the feeding grounds between Areas III east and VI west do not comprise a single population [43]. The most recent genetic study used mtDNA control region sequences (340 bp) and msDNA (12 loci) [12] to examine a total of 2254 samples in the Indo-Pacific sector of the Antarctic: Area III east = 564; Area IV west = 734, Area IV east = 74, Area VE east = 478, Area VI west = 404. The samples were obtained in the Southern Hemisphere summer season in different years. The degree of spatial and temporal divergence was estimated via the F_{ST} and by the randomized chi-square Test of Independence [44]. Results of the heterogeneity tests for both markers showed statistically significant genetic differences between whales in the most distant sectors, western (35°- 130°E) and eastern (165°E - 145°W) (see **Figure 5**), confirming that different populations inhabit the Indian and Pacific sectors of the Antarctic. A simulation study on the dynamics of the species showed that both populations had a soft boundary in the sector 100°-165°E [45].

The main conclusion of the studies was the existence of at least two populations in the feeding grounds of the Indo-Pacific sector of the Antarctic and a transition area in the region around 100°-165°E, across which there is an as yet undetermined level and range of mixing (**Figure 6**). The following names were proposed for these populations: Eastern Indian Ocean Population (I-Population) and Western South Pacific Ocean Population (P-Population) [42].

A recent study described a paternity method based on msDNA (12 loci) to estimate the abundance of mature male Antarctic minke whales in the Indo Pacific sector of the Antarctic using a maximum likelihood approach [46]. Results for the geographical distribution of mother/fetus-father pairs were generally consistent with

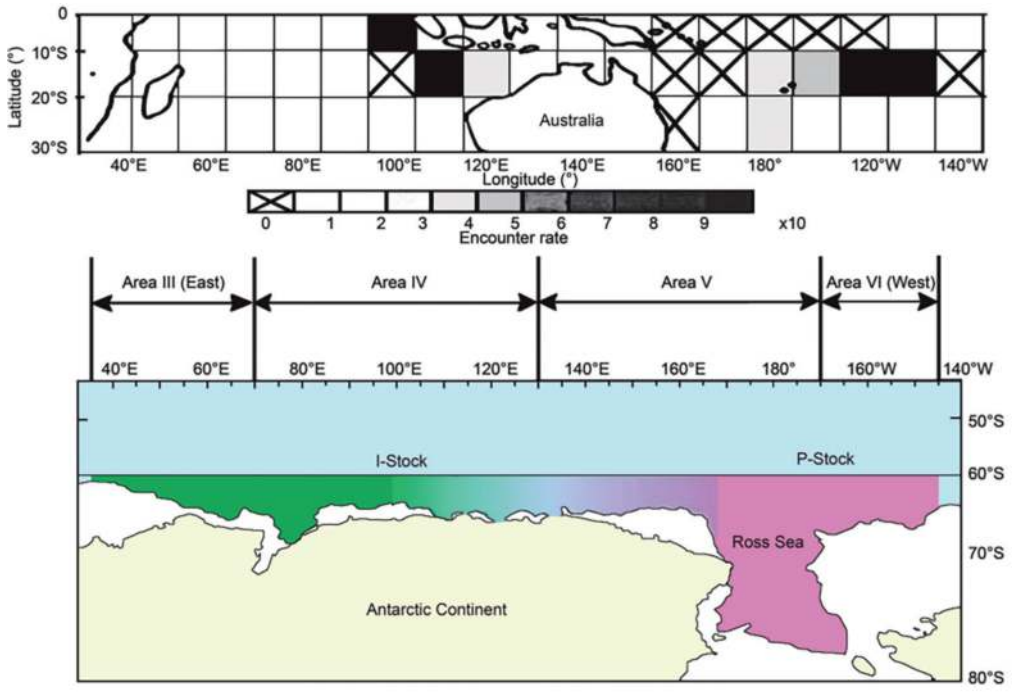

Figure 6.
The current hypothesis of population structure of the Antarctic minke whale. At least two populations occur in the Indo-Pacific sector of the Antarctic covered by the surveys of the JARPA/JARPAII, which mix in a transition area, whose position and extension varies by year and sex. These populations are possibly related to breeding grounds in lower latitudes evidenced by high-density areas suggested by sighting surveys (upper part of figures) (after [42]).

the hypothesis of separate I- and P- Populations because eight of 10 pairs were found in the expected areas of distribution of either population. Only two pairs were found in distant areas.

The genetic studies showed no concordance between the geographic boundaries of the IWC management Areas and the geographical distribution of the I- and P- populations suggested by the genetic analyses.

4.2 North Atlantic common minke whale

The IWC's management areas for North Atlantic common minke whales are shown in **Figure 7**. In this section, the most recent genetic studies on population structure are summarized [47–49]. These studies were focused on examining the biological validity of the management areas in **Figure 7**.

The first study reviewed here [47] was based on genetic samples (n = 306) collected throughout the North Atlantic (see **Table 1**). Samples were collected in spring-summer over several years. The genetic markers used were mtDNA control region (500 bp) and msDNA (16 loci). The analytical procedures used for mtDNA were the F_{ST} for haplotype frequencies and the PHI_{ST} [50]. MsDNA variation was analyzed by testing for homogeneity of allele frequencies among populations using GENEPOP [51] and F_{ST}. Based on the combination of several approaches the authors suggested the existence of four genetically differentiated populations: (1) West Greenland; (2) Central North Atlantic-East Greenland-Jan Mayen; (3) North East Atlantic including Svalbard, the

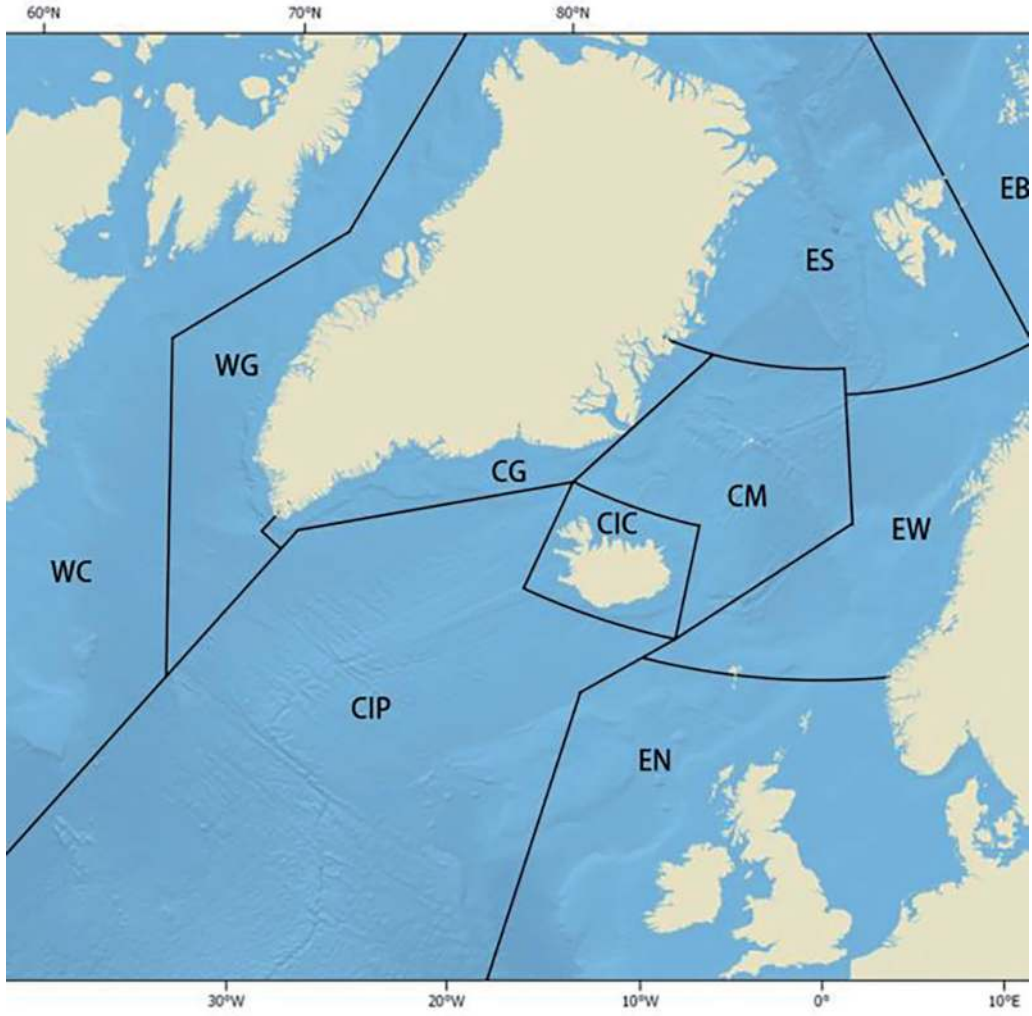

Figure 7.
Management subareas used by the International Whaling Commission for the management of commercial and aboriginal subsistence whaling of North Atlantic common minke whales. Sub-areas prefixed by W represent the western North Atlantic, sub-areas prefixed by C represent the central NorthAtlantic and sub-areas prefixed by E represent the eastern North Atlantic. Management subarea EC mentioned in the main text merged into a single EW subarea.

Barents Sea and north western Norway, and (4) the North Sea. Unlike the other areas, there was a lack of inter-annual variation in West Greenland. The authors postulated that each population evolved in response to regional differences in ecological conditions, namely oceanography, ice cover, prey type and prey availability [47].

The second study [48] was based on smaller sample size (n = 202) but again throughout the North Atlantic (see **Table 1**). Samples were collected mainly in spring-summer over several years. The genetic markers used were mtDNA control region sequences (345 bp) and msDNA (10 loci). The relevant analytical procedures to investigate population structure based on msDNA were the F_{ST} and Rho_{ST} [52]. Also, the study estimated the most probable number of putative populations (K) using *STRUCTURE*. To facilitate the interpretation of the *STRUCTURE* output, a measure based on the second order rate of change of the likelihood function with respect to K was plotted [53]. The F_{ST} and Rho_{ST} were calculated for the population suggested in

Management Area	Sample size study [47]	Sample size study [48]	Sample size study [49]
Western NA	**166**	**51**	**0**
WG	166	36	
WC		15	
Central NA	**54**	**17**	**48**
CIC			
CG + CM	54	17 (CM only)	48 (CM only)
Eastern NA	**86**	**131**	**2596**
ES, EB, EC	63	48 (ES only)	1583 (ES + EB only)
EW			1013
EN	23	83	
Other	**0**	**3**	**0**
Spain		3	
TOTAL	**306**	**202**	**2664**

Table 1.
Summary of sample sizes by North Atlantic management subareas in the three studies referred to in the text.

STRUCTURE using the same methods used for the geographical comparisons. The analytical procedures for mtDNA were the same F_{ST} and PHI_{ST} used in the previous study, which was calculated for the populations inferred from the *STRUCTURE* in the same way as for the geographic comparisons. The study found no evidence of geographic structure comparing putative populations in recognized management areas. However, based on the results of individual genotypes and likelihood assignment methods, the authors identified two putative 'cryptic' populations (populations exhibiting some level of genetic structure, which cannot be explained by past or current barriers to dispersal alone) distributed across the North Atlantic in similar proportion in different regions. They suggested that common minke whales range extensively across the North Atlantic seasonally, but segregate to some extent on at least two breeding grounds [48].

The third study [49] was based on much larger sample size (n = 2664) but primarily from the Eastern North Atlantic (**Table 1**). The genetic markers used were mtDNA control region sequences (331 bp) and msDNA (10 loci). The study used several analytical procedures to investigate population structure based on msDNA including *STRUCTURE*, BAPS (Bayesian Analysis of Population Structure) [54] and traditional F_{ST} and R_{ST} [55]. Genetic differentiation among management areas per year, and the level of temporal population genetic differentiation were tested using the Analysis of Molecular Variance (AMOVA) [56]. The possibility of cryptic populations suggested in the previous study [48] was investigated using *STRUCTURE* and two different outgroups. For mtDNA, the relevant analyses on population structure were based on AMOVA. The authors summarized their findings as follows: no spatial or temporal genetic differentiation was observed for either class of genetic marker; mtDNA identified three distinct lineages without any underlying geographical pattern; nuclear markers showed evidence of a single panmictic population in the eastern North Atlantic. Results of additional simulation analyses suggested that clustering methods may spuriously reveal cryptic genetic structure [49].

4.3 North Pacific common minke whale

The IWC's management sub-areas for North Pacific common minke whales are shown in **Figure 8**. At least two populations of the common minke whales have been historically recognized in the western North Pacific, (1) the Okhotsk Sea-West Pacific (known in IWC literature as the O-stock) and (2) the Sea of Japan-Yellow Sea-East China Sea (known as the J-stock). There are morphological and reproductive [57, 58] as well genetic [59, 60] characters differentiating these two populations.

Recent genetic work has focused on refining this two-population hypothesis as well as investigating whether additional structure exists within the J- and O-stocks. Studies have been based on samples collected mainly during the Japanese Whale Research Programs under Special Permit in the western North Pacific, Phases I and II (JARPN and JARPNII) and bycatches along the Japanese coast. Surveys of these research programs were conducted systematically in the western North Pacific in spring-summer from 1994 to 2016. **Table 2** summarizes the number of samples used in recent studies, by subarea.

Individual probability assignment to either J- or O-stocks was made possible by the use of *STRUCTURE* in a study that examined 4275 samples obtained from JARPN/JARPNII and by-catches in the subareas shown in **Figure 8** and **Table 2**, using mtDNA control region sequences (487 bp) and msDNA (16 loci) [61]. Statistical tests were conducted to investigate deviations from expected Hardy–Weinberg genotypic proportions and *STRUCTURE* was used to determine *K,* the most likely number of genetically distinct populations present in the samples. Regarding mtDNA, the genealogy of haplotypes was estimated using the neighbor-joining method. Twelve of the 16 msDNA loci showed significant deviation from the expected Hardy–Weinberg

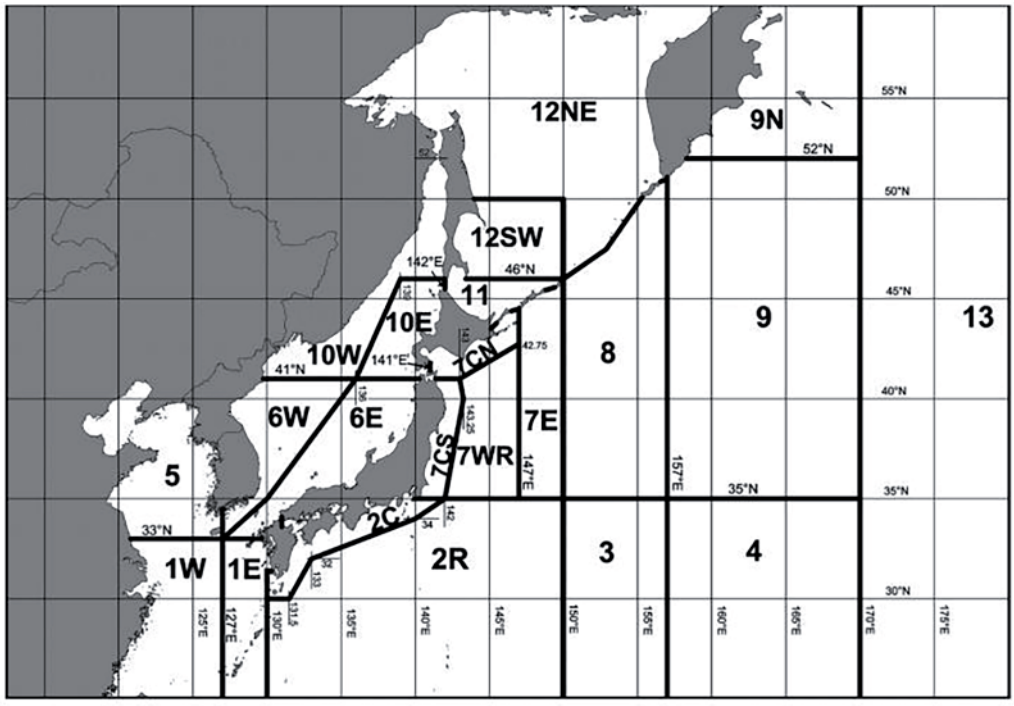

Figure 8.
Management subareas defined by the International Whaling Commission for the management of the North Pacific common minke whales.

Management Area	Sample size study [61]	Sample size O-stock study [62]
2C	487	
6E	717	
10E	13	
11	129	48
7CN	1066	739
7CS	921	439
7E	49	45
7WR	100	89
8	252	223
9	541	487
TOTAL	**4275**	**2070**

Table 2.
Summary of sample sizes by North Pacific management subareas used in recent studies referred to in the text.

genotypic proportions. The inbreeding coefficients were all positive suggesting a homozygote excess. This deviation suggested the existence of individuals from multiple populations in the sample set. The *STRUCTURE* analysis presented the highest likelihood probability at $K = 2$. These results indicated that the samples came from two genetically distinct populations, the J- and O-stocks. **Figure 9** shows the distribution of J and O-stock individuals by sub-area. Almost all the individuals from the Sea of Japan (sub-areas 6E, 10E) were assigned to J-stock, whereas almost all individuals from the offshore North Pacific (east of area 7WR) were assigned to O-stock. Intermediate areas (7CN, 7CS, 11) contained individuals from both stocks. Area 2C on the Pacific side of Japan is mainly occupied by the J-stock individuals.

Figure 10 shows the temporal distribution of the J- and O-stock individuals on the Pacific side of Japan (2C, 7CN and 7CS) expressed as a three-month moving average. In sub-area 2C, J-stock animals are predominant throughout the year. In sub-areas

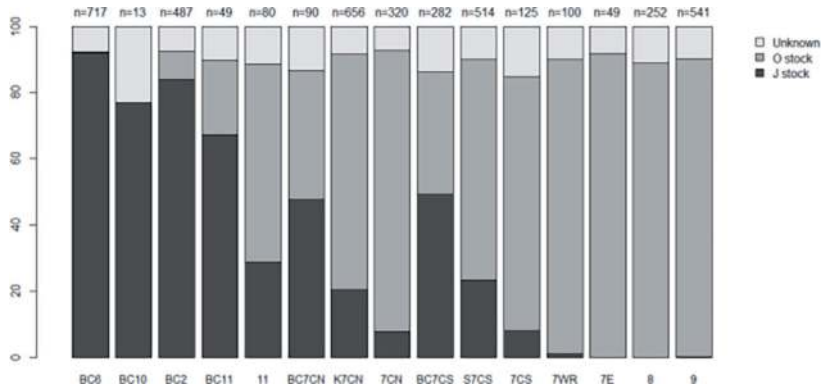

Figure 9.
Spatial occurrence of O- and J-stocks in management sub-areas around Japan (see **Figure 8***). BC2, BC6, BC7CS, BC7CN, BC10, BC11 = bycatches from the respective areas; K7CN = coastal JARPN/JARPNII surveys at Kushiro; S7CS = coastal JARPN/JARPNII surveys at Sanriku; 7CS, 7CN, 7WR, 7E, 8, 9 and 11 = offshore JARPN/JARPNII surveys. Sample sizes are at the top of each bar. 'Unknown' refers to individuals that could not be assigned to either stock by STRUCTURE (after [61]).*

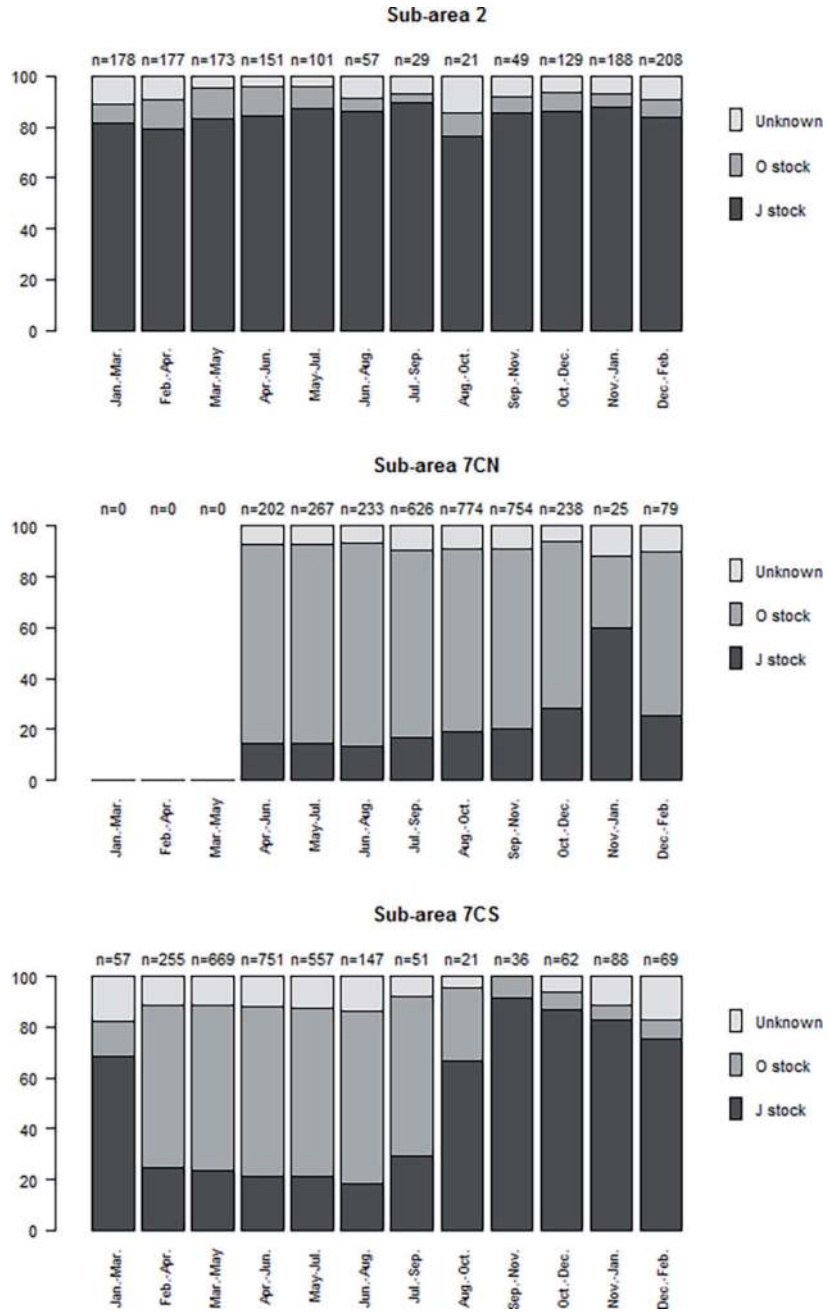

Figure 10.
Monthly occurrence of O- and J-stocks in areas 2C, 7CS and 7CN. Each bar is expressed as three-month moving average. Sample sizes are on the top of each bar. The sampling years in area 2C was 2001–2014; in areas 7CN and 7CS was 1994–2014. 'Unknown' refers to individuals that could not be assigned to either stock by STRUCTURE (after [61]).

7CS and 7CN, the proportion of the J-stock increases in autumn/winter and decreases in spring/summer – the reverse is true for O-stock animals.

The phylogenetic tree of haplotypes showed no population-specific clade although most of the individuals assigned to the J-stock shared the same clade. Most of the individuals assigned to the O-stock shared clades where the J-stock individuals were less frequent [61].

A subsequent study investigated the possibility of additional structure within O-stock based on mtDNA control region sequences (487 bp) and msDNA (16 loci) [62]. The sample size of the O-Stock for the different subareas shown in **Figure 8** was 2070 (**Table 2**). The methods used for investigating structure based on msDNA data were the probability test [63] and the discriminant analysis of principal component (DAPC) approach [64]; for the latter analysis, both J- and O-stock assigned individuals were used. For mtDNA, heterogeneity tests in haplotype frequencies among the samples were conducted using both the chi-square test of independence and conventional F_{ST}. Results based on both markers and different groupings of the samples showed no evidence of sub-structuring within O-stock. A simulation exercise showed that the statistical power of the homogeneity test was high. The DAPC showed clear differentiation between J- and O-stocks but no evidence of sub-structuring within the O-stock sample [62].

A later study used DAPC and spatial analysis of principal component (sPCA) [65] to investigate population structure [66]. The study was based on msDNA (16 loci) and the sample sizes were similar to the previous study [61]. The DAPC failed to find evidence of additional structure other than the J- and O-stocks. The results indicated a low possibility that multiple stocks exist (other than the J- and O-stocks) with overlapping geographic ranges.

A different approach was used in a study that used msDNA data at 16 loci in 4554 whales to infer Parent-Offspring (P-O) relationships using a Maximum-Likelihood approach [67]. Biological information such as the sex and sexual maturity of the whales was used to interpret the genetic results on P-O pairs. The relationship between False Discovery Rate (FDR) and Power (P) was evaluated by simulation. Of 145 inferred P-O pairs (estimated FDR = 0.1), 141 were further evaluated by typing 10 additional msDNA loci. A total of 75 were confirmed (among them 26 Mother-Fetus pairs) and 66 pairs were ranked 'False Positives', yielding an overall observed FDR of 0.468. Among the validated P-O pairs, O-stock pairs were significantly overrepresented and no pairs between J- and O-stock individuals were detected. J-stock animals seem to appear on both sides of Japan closer to the coast, while O-stock individuals occur mostly to the east of Japan, both close to the coast and far offshore. The study provided no evidence for further population structure other than J and O-stocks.

Most recently, a study [68] used three spatially explicit clustering tools including GENELAND [69], TESS [70, 71] and BAPS to explore the msDNA data used previously in [66]. The authors believed that the most informative approach was GENELAND using the mixture model with correlated allele frequency model, which supported $K = 4$, i.e., four putative populations. Given the implications of this in terms of both previous analyses and management strategy evaluation, additional work was subsequently undertaken [72, 73]. That study examined the correspondence of the four above four clusters with the available genetic and non-genetic information. The authors concluded that the most plausible scenario was for two populations (J and O) with complex spatial and temporal mixing along the Pacific coast of Japan [72, 73]. They further noted that some of the analyses conducted were consistent with a scenario of coastal areas containing genetically admixed individuals, and recommended further analyses under the GENELAND as well under the TESS and BAPS.

4.4 Summary and suggestions for future work

Over the last two decades, several important genetic studies focused on investigating population identification and structure in minke whales have been undertaken in three oceanic basins using two genetic markers, mtDNA and msDNA. The driving

force behind these analyses was obtaining information to help with effective conservation and management. Of necessity, all of these studies were based on genetic samples collected in feeding grounds and migratory corridors. In this context, population identification is associated with the concept of Management Units (MUs) described by one author in 1994 as 'populations with a significant divergence of allele frequencies at nuclear or mitochondrial loci, regardless of the phylogenetic distinctiveness of the alleles' [37]. Several of the studies described above presented statistical results that are consistent with this criterion for defining the population. In addition to hypothesis testing, several increasingly sophisticated clustering approaches have been used for the purpose of identifying populations.

Recent studies in the Southern Hemisphere were concentrated in the Indo-Pacific sector of the Antarctic where a large number of genetic samples of Antarctic minke whales was available from Japanese whale research programs. At least two populations have been identified in this sector, the I- and P-populations, which may be related to breeding grounds in lower latitudes of the eastern Indian Ocean and western South Pacific. These populations exhibit significant differences in their mtDNA haplotype and msDNA alleles frequencies, matching the criterion for Management Unit defined above. The Australian continent may play a role in isolating these populations during the winter breeding season, with whales presenting some degree of fidelity to particular feeding grounds in the Antarctic during summer. Although, a transition area of mixing of these two populations was postulated in the Antarctic feeding grounds, whales from each population appear to return to their respective breeding grounds in winter.

To fully understand population structure in the Southern Hemisphere, additional effort should be made to collect genetic samples from other sectors of the Antarctic and other regions of the Southern Hemisphere. This will allow investigation of the full distribution of the P- and I-populations as well the research into structure in the remaining sectors of the Antarctic. Clearly, any understanding of population structure will be greatly facilitated by dedicated efforts to investigate the migration routes and locations of breeding areas; satellite tracking will be an extremely valuable tool in this regard [74].

In the North Atlantic, the results of several genetic studies on population identification and structure may appear contradictory. While some studies suggested subtle genetic differences among groups of whales, others studies based on larger sample sizes have failed to detect any evidence of structure in this oceanic basin. As in the Southern Hemisphere, research on migratory routes and locations of breeding grounds is required to assist the interpretation of the results of the genetic analyses in the feeding ground and migratory routes.

In the North Pacific, recent genetic analyses have been concentrated in the western side due to a larger availability of genetic samples from the Japanese whale research programs and to management needs within the context of the IWC's Scientific Committee. Historically two populations have been recognized in the western North Pacific, the J- and O-stocks, and recent genetic analyses have confirmed their existence and furthermore have revealed more information on their patterns of spatial and seasonal movement. The J-stock occurs mainly in the Sea of Japan although some individuals migrate seasonally to the Pacific side of Japan. The O-stock is mainly found on the Pacific side of Japan. The objective of most recent studies has been to whether or not additional structure occurs within either or both of the J- and O-stocks, and several new analytical approaches were used to respond that question. Results of most of the approaches indicated a lack of additional structure, other than that attributed to the J- and O- stocks. The most recent IWC Scientific Committee discussions allocated high plausibility to the

hypothesis of two populations with spatial/temporal mixing in the western North Pacific [75]. As for the other two ocean basins, effort should be made to collect and analyze genetic samples from the less understood eastern North Pacific as well to undertake focused research to understand migratory corridors and breeding ground locations.

It is also important to make effort to investigate the occurrence, distribution and population structure of common minke whales distributed around Chinese and Korean Peninsula waters, and the genetic relationship with whales distributed in the subareas around Japan. Investigation of the population genetic structure in those waters is important as several annual bycatches have been reported for the Korean Peninsula.

5. General conclusions

Many genetic studies on minke whales were conducted in the last 20 years. New taxonomic information post-1998 relates primarily to the Southern Hemisphere common minke whales (dwarf minke whales) from the western South Pacific and western South Atlantic, which are differentiated by both mtDNA and msDNA markers. The paraphyletic relationship between the North Atlantic and Southern Hemisphere (WSA) common minke whale has important implications for the taxonomic definition of common minke whales. Regarding population genetic structure, at least two populations of the Antarctic minke whale have been identified in the Indo-Pacific sector of the Antarctic, and at least two populations were confirmed in the western North Pacific common minke whales. In the North Atlantic genetic studies suggest that population structure, should it exist, is rather subtle. As for the North Pacific and Southern Hemisphere, analyses are hindered by a lack of knowledge (and thus samples from) breeding grounds.

The population structure of minke whales is intertwined with some degree of fidelity to specific feeding grounds. This fidelity could vary depending on changing short- and long-term environmental conditions. In the case of the Antarctic minke whales, the pattern of distribution and movement of different populations in the feeding grounds has been related with the distribution of their key prey species, the krill (*Euphausia superba*), which in turn depends on the bottom topography as well sea ice and hydrographic features [12]. A similar story has been identified for both the North Atlantic and North Pacific and it is not surprising that feeding ground distribution reflects prey distribution. Future studies on population structure and distribution of minke whales should consider information on environmental variables especially under a scenario of climate change.

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Conflict of interest

All authors declare that there is no conflict of interest.

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